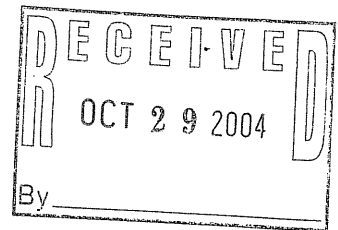


Ecosystem effects of the invasion of Eurasian watermilfoil (*Myriophyllum spicatum*) at
Lake Tahoe, CA-NV

By

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were highly variable, but all sites supported growth of *M. spicatum* except those exposed to extreme wave action. Plants grew as well in non-invaded sites as sites currently invaded. Key environmental characteristics that influenced the success of *M. spicatum* included biologically available phosphorus (SRP) and $\text{NO}_3\text{-N}$ in sediment pore water, and SRP in lake water.

Myriophyllum spicatum may potentially have a more negative effect on water quality at Lake Tahoe than does the native plant, *E. canadensis*, by leaking phosphorus from its shoots during growth and senescence and enhancing the growth of phytoplankton. *Myriophyllum spicatum* and *E. canadensis* were grown hydroponically in clear Plexiglas microcosm tubes containing 1 liter of filtered lake water in laboratory growth chambers set for long-day (14 hours) and short-day (10 hours) photoperiods. The purpose of short-day photoperiods was to induce senescence. Carrier free radioactive $^{32}\text{PO}_3^{4-}$ (10.5 μCi) was introduced to root compartments of *M. spicatum* and *E. canadensis* and sealed off from shoot compartments. Over a 45-day period, release from plant shoots into the water column was significantly greater by *M. spicatum* than *E. canadensis*. Photoperiod did not affect plant growth or phosphorus release.

In an outdoor microcosm experiment, *M. spicatum* and *E. canadensis* plants were rooted in sediment without radioactive $^{32}\text{PO}_3^{4-}$ and grown in 1.5-litre clear Plexiglass tubes for 6 weeks under natural temperature and light conditions. Concentrations of nutrients (total phosphorus and nitrate) and chlorophyll-*a* were higher in microcosms containing *M. spicatum* than those with *E. canadensis* and control treatments that contained sediment and lake water, but no plants. Similarly, a laboratory bioassay study showed that water from containers in which *M. spicatum* was grown

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I dedicate this thesis to my father, who first whet my curiosity in science, and who instilled in me a love for the Sierra Nevada.

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CHAPTER 1

ECOLOGY AND SPREAD OF EURASIAN WATERMILFOIL (*MYRIOPHYLLUM SPICATUM*), AT LAKE TAHOE, CA-NV

illustrates this pattern for *M. spicatum* at Lake Tahoe with an autofragmentation stage also occurring in September. The only locations used in this study that support *M. spicatum* and form substantial ice cover in the winter at Lake Tahoe were Tahoe Keys Cove East Lagoon parts of Meeks Bay Marina. Following ice out in the spring, new stems of plants rise from the dormant stands that had subsided and decayed.

Like many invasive aquatic plants, success in colonization and competition depends on the plant's mode of reproduction. Although *M. spicatum* is an angiosperm capable of seed production, the spread of *M. spicatum* occurs primarily vegetatively through stolon and fragment production (Smith and Barko, 1990; Madsen and Smith, 1997). Two types of fragmentation exhibited by *M. spicatum* are autofragmentation and allofragmentation. Autofragmentation refers to the self-induced abscission of shoot apices that commonly occurs following peak biomass (Madsen and Smith, 1990), while allofragments are formed as a result of mechanical disturbances such as cutting by boat propellers, harvesters, wave action, or crayfish grazing (Flint, 1975). Fragments are easily transported within and between water bodies (Fig. 1.3). They often establish dense stands in areas protected from extreme wave actions, such as the marina of large lakes. Factors known to affect the growth of *M. spicatum* in many mesotrophic and eutrophic lakes are presented in Table 1.1 modified from Smith and Barko (1990).

With regards to nutrient cycling, macrophytes can have important effects on the nutrient budgets in lake sediments and water. Results of several studies suggest that macrophytes are capable of significant depletion of pools of nitrogen and phosphorus in sediments (Prentki, 1979, Barko *et al.*, 1988, Chen and Barko, 1988), and may thereby be a net source of nutrients into the water column of a lake. These nutrient fluxes often lead

the littoral zone of Tahoe is relatively narrow, the effects of macrophytes on clarity of the whole lake is not known. Colonization of the invasive *M. spicatum* in numerous sites around the lake may play an important role in the eutrophication of near-shore areas of Lake Tahoe. This chapter assesses characteristics of water quality in relation to surveys of *M. spicatum* growth in Lake Tahoe, while Chapter 2 considers the role of *M. spicatum* in nutrient cycling and water quality at Lake Tahoe through laboratory and *in situ* experiments. Studies in this chapter concern the current distribution and potential for spread of *M. spicatum* at Lake Tahoe through whole-lake surveys and an *in situ* transplant experiment. Lake surveys also provide a basis for understanding the ecology of *M. spicatum* in its natural ultra-oligotrophic lake environment. Summaries and objectives of this research are described below.

Lake surveys

Aerial and boat surveys of *M. spicatum* populations along the littoral zone of Lake Tahoe, conducted annually by the USDA/ARS beginning in the summer of 1995, indicate that *M. spicatum* has spread rapidly in Lake Tahoe (Anderson and Spencer, 1996). We used this data set as a base to gather more detailed information on the current distribution and spread of *M. spicatum* through aerial, boat and SCUBA surveys in the summers of 1999 and 2000. By establishing permanent transects in four of the survey sites, we aimed to assess changes in growth patterns of *M. spicatum* and native plants over the summer 1999 growing season. Differences in water quality and environmental growth conditions in areas with and without plants were also compared at four survey sites. Specific hypotheses for the survey study included:

Materials and Methods

Lake surveys

Aerial, boat, and SCUBA surveys were conducted to monitor the current distribution of *M. spicatum* populations around Lake Tahoe. Locations of *M. spicatum* in June, 2000 are presented in Figure 1.6, while GPS coordinates of all aquatic plants in Lake Tahoe proper (unmapped) are listed in Appendix 1.1. Figure 1.4 shows typical *M. spicatum* infestations in Lake Tahoe marinas.

We established 35-meter permanent transects across plant communities (water depth 3-3.5 m) at four nearshore locations: Meeks Bay, Emerald Bay, Crystal Shores, and Obexer's Marina. Crystal Bay Marina is a small, private marina with little boat traffic located on the north shore of Lake Tahoe. Obexer's Marina is the most heavily used marina in the study and is located on the west shore of the lake. A creek flows through Meeks Bay marina, on the west shore, intersecting our permanent transect. Emerald Bay, located on the southwest shore, was the only non-marina site. This survey site is located in an isolated bay and accessible only by boat. A stream flows into the lake a few meters south of the permanent transect. We sampled the Tahoe Keys Cove East Lagoon at various times throughout the study as a comparison to the survey sites in the lake proper. The Tahoe Keys, believed to be the origin of the infestation, has the largest population of *M. spicatum* at Lake Tahoe (Fig. 1.7). With the daily mechanical harvesting of aquatic weeds (Fig. 1.2), the Tahoe Keys is likely a source for further spread of *M. spicatum* fragments around Lake Tahoe. We conducted our studies at Cove East Lagoon because it currently is a relatively undisturbed section of the Tahoe Keys without harvesting located

Parameter Water Quality Monitor (Sonde Model 600XL hooked up to a Model 610 DM field display) was used to measure temperature, pH, and dissolved oxygen at 0.5-meter increments. Light extinction at mid-day was determined using an integrating quantum/radiometer/ photometer LiCor (LI-188B) in July, and spherical quantum sensor (LI-193SA) in August, September and November. Light was measured in open water and in areas of *M. spicatum* vegetation under sunny, windless conditions and standardized as the percent of the surface light levels.

On each survey date, we collected interstitial sediment water by SCUBA in areas with and without plant growth. The sampling apparatus (modification of K.L. McKee's interstitial water sampler) consisted of syringes and plastic tubing (Fig. 1.9). Lake water was collected with a Van Dorne water sampler from areas with and without plants into pre-washed (with dilute hydrochloric acid) plastic bottles. Water was collected at depths above the plant canopies with care not to disturb the plants or their periphytic growth. All interstitial sediment and lake water samples were stored in a cooler for transport to the lab. A fraction of each sample (120 ml) was filtered with GF/C glass microfiber filters for soluble nutrient analyses. Filters were folded face-in and kept frozen for chlorophyll-*a* analysis.

Sediment cores of 15 cm depth (6.25 cm diameter) were collected with PVC pipe via SCUBA from areas with and without plants (Fig. 1.10). Sediments were dried for particle size analysis, and ground for total organic carbon content (TOC), nitrogen and phosphorus analyses.

containers of local sediments. Five plants, each with one apical meristem, were placed in a container, and treatments were replicated four times. Containers were placed on the bottom of the lake at depths of 10-12 feet (Fig. 1.12). Following nine weeks of growth, we retrieved containers from transplant sites (October 23, 1999).

Plant survivorship and growth were determined according to the number of surviving plants out of five (% recovery) and plant height. The number of stems on each surviving plant was counted and the total dry weight of all surviving plants measured in each treatment (data not presented). To characterize environmental factors related to plant growth at each site, lake sediment and water were sampled at the beginning of the study. Dried sediment analyses included particle size, total organic carbon (%TOC), total Kjeldahl nitrogen (TKN) and biologically available phosphorus, (Olsen-P). We also measured dissolved phosphorus (DP), soluble reactive phosphorus (SRP), $\text{NH}_4\text{-N}$, and $\text{NO}_3\text{-N}$ of interstitial sediment water. Lake water analyses included total phosphorus (TP), SRP, DP, $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and chlorophyll-*a*. We also measured light, pH, DO, and temperature at the different sites. Due to differences in sampling dates and times between sites, however, we could make only limited use of these data.

Laboratory analyses of biogeochemical components

Chemical analyses of lake and sediment pore water included soluble reactive phosphorus (SRP), dissolved phosphorus (DP), total phosphorus (TP), ammonium-nitrogen ($\text{NH}_4\text{-N}$), and nitrate-nitrogen ($\text{NO}_3\text{-N}$). Analyses were conducted in the Lake Tahoe Research laboratory following standard protocols for low level, calorimetric nutrient analyses. We used a modification of the Indophenol method for $\text{NH}_4\text{-N}$ reported

detection system). This method is based on the analysis originally described by Dumas (1831) and modified by Pella (1990). Plant phosphorus was determined according to a quantitative analysis that utilizes a nitric acid/ hydrogen peroxide microwave digestion described by Kingston and Jassie (1986) and later modified by Sah and Miller (1992). Plant tissue phosphorus was analyzed by atomic absorption spectrometry (AAS) and Inductively Coupled Plasma Atomic Emission Spectrometry ICP-AES with a detection limit of approximately 0.05%.

Statistical Analyses

Lake surveys

Plants

Three-way ANOVA with an interaction and nesting of transect points at sites was used to determine differences in the height of *M. spicatum* based on survey date, site, and individual permanent transect points. The same models was used on *ln*-transformed density data. Changes in root and shoot biomass and root:shoot ratios of *M. spicatum* plants harvested from the four survey sites on four sampling dates were determined by ANOVA using a *ln*-transformation to meet the assumption of normality. The same model and *ln*-transformation were used to look at the effects of site and date on the biomass of whole-plants as well.

We determined differences in the nutrient content of plant tissues using two-way ANOVA with site*date and root/shoot main effects. A loss of plant sample from Emerald Bay during the September sampling date resulted in an unbalanced experimental design. Because the interaction Site*Date was significant for each of these nutrients, analysis of data required that we concatenate Site and Date. Typical Bonferroni pairwise

where E_o is the light at the surface and E_z is the light at depth, z . All measurements were taken in the water column above the plant canopy.

Analysis of covariance (ANCOVA) with 2-way interactions established differences in dissolved oxygen in lake water according to survey site, date, water depth, and the presence or absence of *M. spicatum* plants within sites. Site*date combinations of lake water temperatures were weighted by depth, and three-way ANOVA run on *ln*-transformed temperature data.

Particle size analysis on sediments from the four survey sites and the Tahoe Keys Cove East Lagoon was determined according to the percent of silt, sand, and clay in sediments (Gee and Bauder, 1979). Despite small sample sizes ($n=2$ or 3), two-way ANOVA was used to assess differences in particle size distributions according to survey sites and the presence or absence of plants at sites.

We used two-way ANOVA with presence or absence of plants (p/x) nested within site to determine differences in the *ln*-transformed percent organic matter (%-TOC) in sediments from areas with and without *M. spicatum* at the four survey sites and the Tahoe Keys Cove East Lagoon. We were also interested in differences in %-TOC in these sediments between early summer, July 7, 1999, and late summer, November 5, 1999.

Three-way ANOVA with interactions was used to test the effects of date, site and the presence or absence of plants on Total Kjeldahl Nitrogen (TKN) in lake survey sediments. A similar model was used to determine differences in the biologically available form of phosphorus in dried sediments, Olsen-P. To meet the assumption of normality (Sokal and Rohlf, 1997), we used the natural-log of TKN and Olsen-P.

produced by PCA with correlation and stepwise multiple regression did not fit the data as well as PCA with covariance. Specific environmental variables identified in PCA with covariance were placed into an ANCOVA model in place of the categorical variables, <site> and <sediment>.

Results

Lake surveys

Plants

During our field surveys we observed that *M. spicatum* reached its peak growth by late August and early September, and that by the late September sampling date plants showed signs of senescence: intense autofragmentation, sloughing off of mature leaves and shoots, color change in stems and leaves from vibrant green to reddish white due to chlorophyll degradation. Autofragmentation among plants resulted in shorter stems of the mature plant, and new fragments were establishing in the sediment by November (Fig. 1.2).

The average height of *M. spicatum* in survey plots differed according to date, site, date*site, and individual permanent sampling points along the transects (ANOVA, $F=11.277_{51,277}$, $p<.0001$). We measured average heights of *M. spicatum* in plots ranging from 5 cm to 89 cm. Figure (1.13) shows that in general, height increased from July 7 (mean height 17.11 cm) to August 31 (mean height 24.19 cm) and September 27, 1999 (mean height 24.67 cm). Plant height decreased at all sites except Meeks Bay by November 5, 1999 (mean height 22.70 cm). Residuals of this data set were normally distributed (Shapiro-Wilk, $W=.984$, $p=.6360$), and details of the ANOVA are presented in Table 1.2.

more diverse sites (Figs. 1.16a, 1.16b). *Myriophyllum spicatum*, the dominant macrophyte at Emerald Bay and Meeks Bay Marina, appears to have increased along transects from July 7, 1999 to September 29, 1999, displacing native macrophytes, *Elodea canadensis*, *Potamogeton* sp., *Utricularia* sp, and *Chara* sp. The subsequent decline in *M. spicatum* on November 5, 1999 at both sites corresponded to increases in the percent cover of native species.

Individual plant biomass differed at the four survey sites and across the four summer sampling dates (ANOVA, $F = 13.048_{14,121}$, $p < .0001$) (Fig. 1.17a). Maximum biomass based on the dry weight of whole plants occurred on September 27, 1999 (0.46 ± 0.31 g DW plant⁻¹). In general, the biomass of shoots was greater than roots. Tukey-Kramer HSD pairwise comparisons revealed that the biomass of plants from Crystal Bay Marina was greater than plants from Meeks Bay, Emerald Bay, and Obexer's Marina. Biomass of plants from the latter three sites, on average, were not different. The model also revealed that the biomass of individual plants was greater in August, September, and November than the biomasses of the July sampling date. Residuals of the model were normally distributed Shapiro-Wilk, $W = .9825$, $p = .5917$).

Figure (1.17b) shows the mean root:shoot ratios (dry weight) of individual *M. spicatum* plants along the transect surveys. Root:shoot ratios ranged from 0.0842 (minimum) to 3.56 (maximum) with a mean of 0.597 ± 0.478 . According to the ANOVA, there was not enough information to detect differences in root:shoot ratios of *M. spicatum* at different sites or sampling dates during this one summer study.

The amount of carbon in plant tissues appeared rather uniform, increasing slightly over the summer at all four survey sites (Fig. 1.18a). Plant tissue nitrogen, on the other

(minimum), 0.30% (maximum), $0.15\% \pm 0.05\%$ (mean). The mean phosphorus content of whole plants was $0.22\% \pm 0.10\%$. Residuals of the model were normally distributed (Shapiro-Wilk, $W = 0.9726$, $p = .1434$).

Ratios of C/N in tissues of *M. spicatum* plants varied according to the site*date interaction and root and shoot plant parts ($F = 10.457_{14,110}$, $p < .0001$) (Fig 1.19a, Table 1.4a). Ratios of C/N ranged from 10.78 to 48.27, and the mean C/N ratio for all plants was 27.23 ± 8.84 . On average, C/N was lower in shoots than below ground roots and fragments (Table 1.4b). Tissues of plants from Emerald Bay had higher C/N than from any of the other sites, when survey date was held constant. Likewise, plants from Obexer's Marina tended to have lower C/N ratios than plants from other sites.

Myriophyllum spicatum collected on November 5, 1999 had a higher ratio of C/N than earlier survey dates at Crystal Bay Marina, Emerald Bay and Meeks Bay Marina. Mean C/N ratios in plant tissues, and Bonferroni pairwise comparisons are given in Tables 1.4a and 1.4b. Residuals were normally distributed (Shapiro-Wilk, $W = 0.9804$, $p = .4492$).

Ratios of C/P in *M. spicatum* plants varied by Site*Date concatenations and root vs. shoot plant parts (ANOVA, $F = 3.48_{15,110}$, $p < .0001$). Due to insufficient plant material, multiple data points were missing from this analysis. According to Figure 1.19b, C/P ratios appear to have increased until September 27, and then to have fallen by November 5, 1999. On average, C/P of *M. spicatum* roots (mean = 184.8 ± 149.7) was greater than that of shoots (mean = 100.8 ± 71.8). Mean C/P ratios in plants according to Site*Date combinations and typical Bonferroni pairwise comparisons are given in Tables 1.5a and 1.5b. Statistically, there were no consistent patterns in C/P ratios according to survey site or date. At Crystal Bay, C/P in *M. spicatum* was greater on August 31, 1999

spicatum roots varied according to combinations of Site and Date (ANOVA, $F = 5.775_{14,54}$, $p < .0001$). Apart from lower C/N in plant roots at Obexer's Marina on November 5, 1999 than September 27, 1999, Tukey-Kramer HSD did not reveal many significant differences by date (Table 1.6b). Mean C/N in roots and shoots are given in Table 1.6c and 1.6d. Although one way ANOVA determined that C/P ratios of *M. spicatum* shoots alone differed according the Site*Date combination (ANOVA, $F = 2.401_{14,58}$, $p = .0101$), there were no significant differences between pairs in Tukey-Kramer HSD contrasts. Mean C/P ratios of plant shoots are given in Table (1.7). There were no differences in C/P of *M. spicatum* roots at different survey sites on the four survey dates.

Through stepwise multiple regression (forward step) and ANOVA we found that the biomass of *M. spicatum* seemed to be associated with TP and $\text{NH}_4\text{-N}$ in lake water, with $\text{NH}_4\text{-N}$ in interstitial sediment, and with Olsen-P in dried lake sediments ($F = 18.754_{8,119}$, $p < .0001$, $R^2_{\text{adj}} = 0.5279$) (Table 1.8a). Correlations were negative for each of these factors except $\text{NH}_4\text{-N}$ in lake water (Table 1.8b). Nutrient concentrations in sediment interstitial water and lake water are presented in Appendices 1.3 and 1.14.

Using stepwise multiple regression and ANOVA, we found that concentrations of nitrogen in *M. spicatum* correlated to $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in sediment pore water and lake water ($F = 28.135_{12,129}$, $p < .0001$, $R^2_{\text{adj}} = 0.6978$) (Table 1.9a). Correlations were negative for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in lake water and positive for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ in sediment pore water (Table 1.9b). Residuals of the model were normally distributed (Shapiro-Wilk, $W = 0.970$, $p = .0697$).

date, 11/5/99 than all of the earlier dates. Chlorophyll-*a* in July was not different at Obexer's from levels in August or September. With marginal significance ($p = .0645$), the August sampling date had a lower chlorophyll-*a* level than the September date. Chlorophyll-*a* did not differ in lake water between sampling dates at Emerald Bay. There were also no differences according to date at Meeks Bay except that chlorophyll-*a* was higher on the November date than in July. Individual measurements of chlorophyll-*a* in Lake Tahoe littoral water are listed in Appendix 1.5.

Light extinction coefficients varied among survey site, on different dates, and in areas with and without plants at certain sites (ANOVA, $F = 8.785_{10,37}$, $p < .0001$) (Fig. 1.21). Although plants vs. no plants (p/x) was not significant as a main effect, we kept it in the model because of its significance in the interaction with site (Table 1.12a) (Neter et al., 1996). Light extinction coefficients were lower on the three earlier sampling dates than on November 5, 1999 (July 7, 1999 mean = 0.275 ± 0.127 ; September 9, 1999 0.244 ± 0.142 ; September 27, 1999 0.180 ± 0.140 , November 5, 1999 0.715 ± 0.035). By site, the highest extinction coefficient occurred at Meeks Bay. Figure 1.21 illustrates that mean extinction coefficients appeared slightly higher in areas with plants than no-plants at Emerald Bay, Meeks Bay, and Obexer's Marina. However, differences in extinction coefficients were not significant at the 5% alpha level, except at Crystal Bay Marina where the no-plants area had a higher extinction coefficient. Specific differences in extinction coefficients between specific pairs of dates, sites, and plant/no-plant areas are presented in Table (1.12b). Residuals of the model were normally distributed (Shapiro-Wilk, $W = .9799$, $p < .0001$). Individual light measurements in the

temperature was greatest at Crystal Bay Marina and coldest at Meeks Bay Marina.

Tables 1.14a and 1.14b give details of the ANOVA and Bonferroni pairwise comparisons of individual factors in the analysis. Individual temperature measurements are given in Appendix (1.8). Although residuals of the model were not quite normally distributed at the 5% alpha level (Shapiro-Wilk, $W=0.970$, $p=.0008$), we accept these results given that there were 341 temperature measurements in the model.

Particle size analysis showed that sand was the largest constituent of sediments, comprising between 87% and 96% of sediment from the four lake survey sites and the Tahoe Keys Cove East Lagoon, while %-silt and %-clay made up between 1% and 9% of sediment composition (Fig. 1.22). With a small sample size ($n=2$), there was not enough power in the two-way ANOVA to reveal differences in %-sand, %-silt, or %-clay between sites or areas with and without plants. Actual particle size measurements are presented in Table (1.15).

We found that the percent of organic matter in sediments (%-TOC) was different among the four survey sites and Tahoe Keys Cove East Lagoon, and depending on the site, %-TOC was different in areas with plants vs. no plants (ANOVA, $F = 11.092_{7,31}$, $p<.0001$) (Fig. 1.23). The amount of TOC did not seem to vary in sediments collected on early and late summer sampling dates. Table 1.16 gives typical Bonferroni contrasts between %-TOC at the five survey sites. On average, areas with *M. spicatum* plants at Crystal Bay Marina ($t = 2.420_4$, $p=.0216$) and Emerald Bay ($t = 2.401_4$, $p=.0266$) had higher %-TOC than areas without plants. However, there was not enough information in the model to determine differences between plants and no plants at Obexer's Marina. Comparing sites, the amount of TOC was greater in the sediments from Obexer's Marina

sediments without plants (Table 1.18b). The opposite was true for sediments from Meeks Bay, and we did not detect differences according to p/x at Emerald Bay. According to the significant Date*p/x interaction in this model, sediments with plants had higher levels of Olsen-P on August 31, 1999 than sediments without plants. By September 27, sediments without plants had higher levels of Olsen-P than sediments with plants. On both July 7 and November 5, 1999, we did not detect differences due to p/x. Due to an imbalanced experimental design, Crystal Bay was not included in the p/x contrast on July 7, 1999. Comparing sites, we found that Olsen-P was significantly lower in Emerald Bay sediments than in sediments from Meeks Bay or Obexer's Marina. Data were *ln*-transformed to meet the normality requirement for ANOVA (Shapiro-Wilk, $W = 0.985$, $p = .7960$).

Soluble reactive phosphorus in interstitial water of sediments was generally quite low and differed by site, date, and the presence or absence of plants at survey sites (ANOVA, $F = 7.387_{22,64}$, $p < .0001$) (Fig. 1.26a, Table 1.19a). Soluble reactive phosphorus in interstitial sediments was highly variable according to date and site. Typical Bonferroni pairwise analysis revealed that SRP in interstitial sediment water was greater on August 31 and September 27 than on July 7 or November 5, 1999 (Table 1.19b). By site, SRP in sediments was greater at Emerald Bay than at any of the other sites. We also found that depending on the site, interstitial sediment SRP was different in areas with and without plants. At each of the sites except Meeks Bay, sediments without plants had higher SRP than areas with plants, although differences were significant only at Emerald Bay and Meeks Bay Marina (Table 1.19b). Although the interaction Date*p/x was significant in the model, typical Bonferroni pairwise contrasts revealed that SRP was

Dissolved phosphorus, the acid digested form of soluble phosphorus in sediment pore water, varied according to site, date, and the presence or absence of plants at the four survey sites (ANOVA, $F = 6.702_{9,56}$, $p < .0001$) (Fig 1.27, Table 1.20a). This analysis excluded the July date due to an inadequate volume of water sampled for chemical analysis on that date. Dissolved phosphorus decreased in sediments over time from August 31, 1999 to November 5, 1999 (Table 1.20b), but differences were not due to the presence or absence of plants. With regards to site, DP in sediments at Crystal Bay was less than in Meeks Bay sediments. Likewise, dissolved phosphorus was greater in sediments at Emerald Bay than at Obexer's Marina (Table 1.20b). Dissolved phosphorus in sediment pore water also differed according to the presence or absence of plants only at Emerald Bay, where sediments without plants had higher levels of DP than sediments that supported plant growth. To compare the DP in sediment from the Tahoe Keys, we specified the August 31, 1999 sampling date, and found that DP was greater in interstitial sediment pore water at the Tahoe Keys than at any other site (Table 1.20b). Data were *ln*-transformed to meet the ANOVA assumption of normality (Shapiro-Wilk, $W = 0.9706$, $p = 0.2874$).

We did not find differences in interstitial sediment $\text{NH}_4\text{-N}$ according to survey site, date, or the presence or absence of plants (ANOVA, $F = 1.100_{22,66}$, $p = 0.3695$) (Fig. 1.28).

The amount of $\text{NO}_3\text{-N}$ in interstitial sediment pore water varied by survey site, date, and the presence or absence of plants at the four survey sites (ANOVA, $F = 3.469_{19,64}$, $p < .0001$) (Fig. 1.29). Although the main effects of date and p/x were not significant, they remained in the model because they play significant roles in interactions

$p < .0001$) had significant effects on the probability of survival of *M. spicatum* in the transplant experiment (Fig. 1.30). Although, the effect of milfoil-source on plant survival was not significant, it was included in the model as a main effect because the interaction site*milfoil-source was significant (Neter et al., 1996). Results of logit parameter contrasts are given in Table (1.22a). Because *M. spicatum* from the Tahoe Keys was transplanted to all four transplant sites (Tahoe Keys, Meeks Bay, Kaspian Point, Boatworks Marina), while *M. spicatum* from Meeks Bay was transplanted only at Meeks Bay and the Tahoe Keys Cove East Lagoon, we contrasted the effects of site on survivorship using only those containers with *M. spicatum* from the Tahoe Keys.

Myriophyllum spicatum grew successfully at every site and in each type of sediment, except where there was extreme wave action outside of the Boatworks Marina. Similarly, there was no successful growth of *M. spicatum* grown in Tahoe Keys sediment at Kaspian Point, a less protected area. The logit contrast analysis of site parameter estimates determined that *M. spicatum* was more likely to survive at the Tahoe Keys than at Meeks Bay or Kaspian Point. There was no difference in the likelihood of survival at Tahoe Keys vs. the Boatworks Marina, where plants were protected from wave action. There was also no difference in the survival potential of *M. spicatum* based on plant-source (Tahoe Keys vs. Meeks Bay Marina).

Among sediments, survivorship of *M. spicatum* was greater in Tahoe Keys sediment than in Boatworks sediment. There were no significant differences in survivorship likelihood between plants grown in sediment from the Tahoe Keys, Meeks Bay, or Kaspian Point (Table 1.22a).

at the Meeks Bay (9.7 ± 1.3) (ANOVA, $F = 28.844_{1,4}$, $p = .0076$) (Fig. 1.32c). At certain sites, the source of sediment influenced the height of *M. spicatum* growth (ANOVA, $F = 13.09_{4,122}$, $p < .0001$); on average, plants grown in sediments from the Tahoe Keys grew tallest (Table 1.23b).

Crayfish appeared to affect the success of transplanted *M. spicatum* in this study. We found that plants grown in their home sites survived crayfish grazing more than plants transplanted from a foreign site. That is, at Meeks Bay, plants from Meeks Bay grew an estimated 21.5-cm taller than those from the Tahoe Keys (Table 1.23b). This can be explained by preferential grazing on Tahoe Keys milfoil by crawfish at Meeks Bay, a phenomenon that we observed during our SCUBA surveys.

We used principle components analysis (PCA) of covariance to identify environmental variables that explained the variation among water conditions and sediments, independent of plant heights, in the transplant experiment. Environmental variables consisted of: $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, DP, SRP, in lake water, and $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, DP, SRP in interstitial sediment water, and TKN, P-Olsen, % TOC, %-Sand, %-silt, and %-clay in transplant sediments. We did not have individual measurements of environmental variables associated with plant heights from each container, so we used means of environmental variables: $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, SRP, DP, and TP in lake water; $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, SRP, DP in interstitial sediment pore water; and TKN, Olsen-P, % TOC, and particle size of dried sediments. Distributions and means of these variables at the various transplant sites are presented in Figures 1.33a-c. The four unique values associated with each variable, representing a mean of each of the four transplant sites or sediment sources, are listed in Appendix 1.10. Principle components analysis identified SRP and

(1999) monitored the expansion of *M. spicatum* in oligotrophic Lake George, N.Y., from 6 m² in 1987 to 144 m² in 1997. From its initial observation in 1985, *M. spicatum* spread to 106 discrete locations in Lake George (Boylen et al., 1996). Spread of *M. spicatum* was impeded only by physical barriers such as water depth limits and sediment type. On a smaller scale, Madsen and Smith (1997) measured radial expansion rates of 3.9 cm day⁻¹ of *M. spicatum* populations in experimental ponds. Although the exact date of introduction to Lake Wingra, WI is unknown, *M. spicatum* increased in abundance over six years (1960-1966), displacing native plants, and becoming the dominant macrophyte in what was once a diverse aquatic plant community (Trebitz et al., 1993). During the peak of its infestation, *M. spicatum* covered about 40 ha of the shallow, eutrophic lake's 140 ha surface. Carpenter (1981) found that poor light penetration limited *M. spicatum* growth to water shallower than 2.5 m at Lake Wingra. As a result, the rate of spread of *M. spicatum* was controlled by the rate of formation of colonizable sediment surface areas in shallow water. Although we did not suspect turbidity to be a limiting factor for the spread of *M. spicatum* in the pristine waters of Lake Tahoe, water clarity was among the many factors considered in our investigation of the ecological parameters determining the spread and growth of *M. spicatum* at Lake Tahoe.

Changes in density, height, and biomass of *M. spicatum* in the lake surveys fit the growth pattern we observed over the summer 1999 survey period (Fig. 1.2). The mean peak biomass of *M. spicatum* at Lake Tahoe survey sites was achieved by September 27, 1999 at 0.46 ± 0.31 g DW plant⁻¹. Given that the average density of *M. spicatum* in Lake Tahoe proper was $261 \text{ stems m}^{-2} \pm 169 \text{ stems m}^{-2}$, the mean biomass at Lake Tahoe can be estimated at 88.74 g m⁻² dry weight. Considering the variation in these measurements,

1999) and 2.5 m at Lake Wingra (Carpenter, 1981). *Myriophyllum spicatum* reached estimated heights of at least a meter in marsh areas behind the Tahoe Keys Marina in 1991, where water clarity was much poorer than Lake Tahoe (data not presented).

Our experiment to test the effects of lower light levels on *M. spicatum* growth using blue polyethylene plastic tarps with UV protection, suggested that plants actually grew taller in the shade (1.16% light of open water) than in the open, clear waters of Crystal Bay Marina. It should also be noted that because this experiment was conducted between piers in a marina, even the open water treatment provided plants some shade as the sun moved across the sky and behind the piers. In truly open water we might have expected differences in plant height to be more pronounced between shade and no shade, especially because plants growing under the shade of boat docks were three times as tall as those in the open of Crystal Bay marina from July throughout August, 1999. In a recent study (2000), Huovinen and Goldman found that *in situ* phytoplankton productivity was hindered by current levels of UV-B radiation at Lake Tahoe. Because we measured the quantity of photosynthetically active radiation (PAR, scalar irradiance) rather than the quality of light at Crystal Bay Marina, we cannot draw conclusions about the properties of light that influenced the growth of *M. spicatum* in this preliminary study. Other studies have found, however, that concentrations of hydrocarbons, which can occur in lake marinas, in conjunction with UV-B radiation, may have deleterious effects on aquatic plant growth (Arfsten et al., 1996; Duxbury, et al. 1997; Huang, X.D., 1997).

Further field observations supported the speculation that *M. spicatum* growth was influenced by light levels at Lake Tahoe. We found that *M. spicatum* grew to the greatest height at Meeks Bay, the site of poorest water clarity, weak light attenuation, and high

to a decade (Trebitz et al., 1993; Madsen, 1994; Boylen et al., 1996, 1999). Distributions of aquatic plants documented in this study can be used as benchmarks for future studies monitoring the effects of *M. spicatum* on native macrophytes.

Nutrient concentrations in plant tissues changed as expected according to the life cycle described for *M. spicatum* over the summer 1999 survey period. Lower C/N ratios in Meeks Bay plant shoots in July support the expectation that young plants concentrate nitrogen in their photosynthesizing shoots early in the growing season (Rorslett et al., 1986; Graneli and Solander, 1988). Nitrogen concentrations in plant tissues decreased from July to the August 31 and September 27 survey dates. Gerloff and Krombholz (1966) explained that decreased midseason values of nitrogen and phosphorus in plants, obtained when plant growth is heaviest, should indicate whether the supply of a particular element has been reduced such that that element becomes limiting for optimum growth of that plant species. The decline in nutrient concentration in *M. spicatum* may be explained by a decrease in sediment nutrient availability during the period of active growth. It is also probable that older plants lost nitrogen in the process of senescence by September 27, 1999. By November, many of the survey plants had senesced, and new plant fragments were being established. Slightly higher N concentrations in plant tissues collected in November may reflect the fact that plants were selected at random for morphological and tissue analyses in surveys. Because we did not separate older senescing plants from the new generation of young plant fragments with high N contents, the combination of cohorts on the November sampling date probably raised the mean N of mature, senescent survey plants on this date. Higher C/P ratios in Crystal Bay *M. spicatum* on August 31 and September 27 than on November 5, may also reflect

difficulties involved with separating different generations as well as live and dead tissues of below-ground plant biomass.

The lack of change in C/P ratios in *M. spicatum* roots and shoots over the course of the summer may be explained by high variability among plants at different survey sites and dates. Because the mean phosphorus concentration ($0.22 \pm .10\%$ dry weight) in *M. spicatum* at Lake Tahoe was greater than the critical concentration established by Gerloff and Krombholz (1966) (0.13% P dry weight), it seems that plants were not limited by phosphorus in the littoral environment, and that luxury consumption (Graneli and Solander, 1988) of phosphorus may have buffered signs of phosphorus translocation in the plants. The question of phosphorus retranslocation between plants roots and shoots was investigated in more detail using a ^{32}P tracer in a separate microcosm experiment described in Chapter 2.

The low mean N/P ratio (8.17) for *M. spicatum* at Lake Tahoe suggests that if *M. spicatum* growth is nutrient-limited, then it is more likely limited by N. The N/P ratio has been used to indicate relative deficiencies of N and P in aquatic plants, phytoplankton and terrestrial species (Chapin and van Cleve, 1989; Royle and King, 1991; Sytsma and Anderson, 1993a, Lambers et al., 1998). The ratio of N/P in plants remains surprisingly constant (8-10.1) when plants receive nutrients in a ratio similar to that in their tissues (Lambers et al., 1998). Deviations from this ratio reflect nutrient imbalance caused by reduced uptake of growth limiting nutrients, which is sometimes also combined with luxury consumption of nutrients that do not limit the growth of plants. Consideration of the lower limits of N concentrations in tissues of *M. spicatum* at Lake Tahoe (mean $1.62\% \pm 0.59\%$), also points to nitrogen limitation for *M. spicatum* in this since the

Obexer's Marina tended to have lower C/N ratios than plants from other sites, implying that their growth was less limited by nitrogen.

In this study we also aimed to establish the relationship between *M. spicatum* biomass and environmental variables at survey sites. We found that TP and $\text{NH}_4\text{-N}$ in lake water, $\text{NH}_4\text{-N}$ in interstitial sediment, and Olsen-P in dried lake sediments had the strongest associations with *M. spicatum* biomass. The negative associations between sediment nutrients and plant biomass might be explained by competition for nutrients in the sediment. Low nutrient availabilities could result from uptake by plants in biomass production and increased microbial activity at that particular time. Graneli and Solander (1988) describe a concentration gradient of dissolved reactive phosphorus in the sediment with the lowest concentrations near roots crowns of aquatic plants. Similarly, extensive reductions in sediment $\text{NH}_4\text{-N}$ in beds supporting *M. spicatum* have been reported (Carignan, 1985). Furthermore, Nichols and Keeney (1976) established that $\text{NH}_4\text{-N}$ was the preferred form of nitrogen by *M. spicatum*. The negative correlation between TP and plant biomass also makes sense since TP incorporates periphytic and planktonic algae in lake water. High abundances of algae in the vicinity of macrophytes implies greater competition for light and nutrients among all primary producers that might reduce plant biomass production (Gross, 1996; Sondergaard and Moss, 1998). Evaluation of the strength of this correlation ($R^2_{\text{adj}} = 0.5279$) should consider that each measure of plant biomass did not correspond to independent measures of environmental variables. Rather, because environmental variables were measured in replicates of $n=3$ or $n=5$, we used means as unique values for combinations of site and date to explain variation in plant biomass. Conclusions from this analysis are speculative, and further experiments should

associations of *M. spicatum* with microbes in the plant-sediment rhizosphere (Wigand and Stevenson, 1997).

Environmental variables

Results of this survey support the hypothesis that differences in environmental variables were with the presence or absence of plants at the survey sites. Concentrations of chlorophyll-*a* followed the pattern observed in lakes of low chlorophyll concentrations in the early summer as plants compete with phytoplankton for nutrients during their early rapid growth period (Sondergaard and Moss, 1998). Increased chlorophyll-*a* concentrations late in the summer may have been due to the senescence of plants and release of nutrients that enhance phytoplankton growth (Landers, 1982). On average, chlorophyll-*a* in lake water was greater in areas with plants than without plants, particularly at the Tahoe Keys Cove East Lagoon, Meeks Bay Marina, and Obexer's Marina. Comparisons of areas with and without plants at the Tahoe Keys Cove East Lagoon may not be valid as the no-plant site was located across a narrow sandbar in the lake proper, rather than in the lagoon itself (Fig. 1.17). The relationship between *M. spicatum* and phytoplankton productivity is described in Chapter Two in a series of microcosm experiments and bioassays using natural Lake Tahoe phytoplankton.

Higher light extinction coefficients in areas with plants (measured above plant canopies) at all of the survey sites except Crystal Bay Marina implies higher turbidity in the water in the presence of plants. This is not surprising given the abundance of epiphytic and planktonic algae and fine sediment and detritus associated with beds of macrophytes (Carpenter and Lodge, 1978; Wetzel and Sondergaard, 1998). Given that

hourly fluxes in DO since the oxygen content of water is related to rates of photosynthesis. Further studies might also use experimental manipulation to test the effects of macrophyte density on DO concentrations in littoral areas of Lake Tahoe.

As expected in an unstratified lake, temperature decreased with depth and increased over time (Horne and Goldman, 1994; Wetzel, 1983). The rise in temperatures in areas with plants on July 7, 1999 through August 30, 1999 and subsequent decrease by September 28, 1999 corresponds to the growth pattern of *M. spicatum* as the plants reached stages of peak height, biomass, and density in August and entered senescence by the end of September. In addition to photoperiod, temperature may be an important environmental cue influencing the life cycle of *M. spicatum* (Smith and Barko, 1990). Although differences in temperature were slight we cannot draw definitive conclusions about the relationship between *M. spicatum* and temperature without controlled experimentation.

We did not find differences in sediment particle size between areas with and without plants. In all cases, sand comprised the largest fraction of sediment (87%-96%) with silt and clay only 1%-9% of the sediment. Contrary to Barko and Smart's (1986) claim that *M. spicatum* does not grow well in coarse, sandy substrate, we found that the distribution of plants at current survey sites may not be confined by such sediment particle size distributions. Barko and James (1998) discuss the ability of aquatic plants to slow water movements, increasing sedimentation rates and influence particle size distribution in lakes. Because there was not a difference in particle size distribution between areas with plants and without plants (keeping in mind a small sample size of $n=2$), it is possible that by 1999 the presence of aquatic plants, primarily *M. spicatum*,

We found that concentrations of SPR decreased over time in areas with plants relative to areas without plants (Fig. 2.27b). This is most likely the result of uptake by plants as plants readily absorb biologically available phosphorus from sediments as part of their active role in P cycling in aquatic systems (Carignan, 1985; Smith and Adams, 1986; Stephen et al., 1997). High variability among results suggests that the small sampling size ($n = 3$) in this experiment did not yield enough power to accurately represent the high heterogeneity of nutrients in sediment pore water at Lake Tahoe.

There were no consistent trends in nutrients, $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, or DP, cycling at survey sites according to the presence or absence of plants over time. It appears that nutrient concentrations in sediment pore water are highly variable. The effects of plants on nutrient cycling might best be detected under controlled microcosm experiments or in the field with large sample sizes (Chapter 2).

Reciprocal transplant

In a study to determine the factors governing spread of *M. spicatum* in Lake Wingra, WI, Kimbel (1982), found that the optimal conditions for colonization were high light availability, high temperature and sediment nutrients, shallow water and organic-rich sediments. In this reciprocal transplant experiment, we determined that *M. spicatum* could grow successfully at every site and in the sediments from every site tested at Lake Tahoe. Only under conditions of extreme wave action did *M. spicatum* fail to grow. Survivorship was highest when plants from a particular location were grown at that location. This could be related to our observation that crayfish preferentially grazed foreign transplants in the transplant experiment. Future transplant experiments could

spicatum. Ratios of N/P in survey plants indicated that *M. spicatum* was nitrogen limited at sites in Lake Tahoe proper. It is possible that the negative association with $\text{NO}_3\text{-N}$ reflects the low levels of this nutrient as *M. spicatum* removes it from sediments and water for growth. Given that we did not have individual measurements of environmental variables for each plant in transplant containers and were forced to use four unique values (averages) in the PCA model to explain variation in transplant sites and sediments, $R^2=0.46$ for this study is not terribly low. However, we recommend repeating this experiment with a more detailed sampling analysis of environmental variables to better determine which variables most strongly affect plant growth.

Conclusions

Our detailed surveys by boat, airplane, and SCUBA during the summers 1999 and 2000 reveal that *M. spicatum*, in addition to its large population in the Tahoe Keys Marina, has spread to 15 sites in the lake proper. The transplant experiment indicated that *M. spicatum* has the potential to spread to further sites that are protected from wave action. Despite the fact that *M. spicatum* grew the tallest at the Tahoe Keys Marina and in sediment from the Tahoe Keys, this invasive plant has the potential to successfully establish at other sites around Lake Tahoe in which it is not currently present. Growth success of transplanted *M. spicatum* was influenced by transplant site and sediment type, and specifically by biologically available SRP in lake water and sediments. Because of the problems associated with this exotic weed, including its potential threat to water quality (Chapter 2), management solutions should be explored.

CHAPTER 2

EFFECTS OF SUBMERSED MACROPHYTES ON WATER QUALITY AT LAKE TAHOE: A COMPARISON OF INVASIVE EURASIAN WATERMILFOIL (*MYRIOPHYLLUM SPICATUM*) WITH NATIVE ELODEA (*ELODEA CANADENSIS*)

nutrients during stages of senescence and decay to overlying water columns (Landers, et al., 1982; Rorslett et al., 1986; Sater et al., 1994).

Accelerated nutrient loading is a great concern for eutrophication in lakes, and the role of submerged macrophytes in the nutritional economy of lakes has inspired many important studies. Submerged macrophytes are unique among rooted aquatic vegetation because they link littoral sediments with the overlying water column (Barko and James, 1998), thereby cycling nutrients, such as nitrogen and phosphorus that can contribute to the process of eutrophication. Over the past 20 years debate over whether macrophytes serve as sources or sinks for particular nutrients has led to studies that attempt to quantify nutrient source-sink relationships involving both soluble and particulate nutrient fractions (Barko *et al.*, 1991; Barko and James, 1998). In general, submersed macrophytes serve as nutrient sinks during their active growth, and as potential nutrient sources during periods of senescence and decay (Carpenter and Lodge, 1986; Rorslett, et al. 1986; Jones, 1990; Sondergaard and Moss, 1998).

Understanding nutrient cycles between sediments and the water column via submerged macrophytes requires determination of the relative contribution of sediment and water to nutrient uptake by submerged macrophytes. Barko *et al.* (1991) presented a simple empirical model to predict the relative contributions of sediment and water to the phosphorus budget of submersed macrophytes. This model predicts that more than 50% of the phosphorus supplied to macrophytes comes from the sediments when the ratio of dissolved reactive phosphorus (DRP) in the sediment interstitial water to DRP in the open water exceeds about 4. Multiple studies reviewed by Barko *et al.* (1991) revealed that this ratio is not uncommon, and that in fact the ratio is often so high that sediments contribute

Dynamics of epiphytes and phytoplankton populations also respond to life cycle patterns of submersed macrophytes (Landers, 1982; Sondergaard and Moss, 1998). Like many submersed macrophytes, *M. spicatum* evolved thin, finely divided leaves to cope with the stress of slow nutrient and gas exchange as well as poor light attenuation in water (Sculthorpe, 1967; Wetzel, 1975). These structures, both alive and senescing, promote the development of a symbiotic attached algal and microbial community (Wetzel and Sondergaard, 1998; Bronmark and Vermaat, 1998). Oxygen, carbon dioxide, nitrogen, phosphates, and silica, along with organic compounds are secreted in small quantities during the photosynthesis process of living plant tissues, and are released in much larger masses during senescent stages of the plant's life cycle (Carpenter and Lodge, 1978; Smith and Adams, 1986; Barko et al., 1991; Jackson et al., 1994). Released nutrients contribute to eutrophication and deterioration of water quality by enhancing the growth of attached and planktonic algae (Carpenter, 1980; Craig and Adams, 1986; Jones, 1990). Landers (1982) demonstrated that autumn senescence of *M. spicatum* contributed 18% of the total annual phosphorus in a P-limited reservoir in Indiana, resulting in significant algal blooms. Other studies used radiolabeled phosphorus to demonstrate that submerged macrophytes, such as *M. spicatum*, obtain most of their phosphorus from sediment, and serve as a source of phosphorus to lakes as they leak nutrients during senescence (Carignan and Kalff, 1982; Moeller et al., 1988; Wetzel, 1996).

The majority of studies on nutrient cycling through *M. spicatum* have been conducted in mesotrophic and eutrophic systems, leaving a paucity of research in ultra-oligotrophic systems, such as Lake Tahoe. The invasion of *M. spicatum* in Lake Tahoe is

day photoperiods in two growth chambers to determine if senescing conditions (short days) resulted in higher levels of ^{32}P leakage compared to plants grown under long days.

Outdoor sediment-plant microcosms and ^{14}C phytoplankton bioassay

In a second set of microcosms (Fig. 2.2), we established *M. spicatum* and *E. canadensis* in sediments outdoors at the time of natural senescence (September 24-October 27) under late summer photoperiods to test the hypothesis that macrophytes facilitate the release of nutrients and stimulate phytoplankton productivity in Lake Tahoe's ultra-oligotrophic water. We hypothesized that *M. spicatum* and *E. canadensis* could change the conditions of water in the microcosm tubes by leaking nutrients. By taking up nutrients from the sediments, and releasing some in the water column, plants could increase the nutrient availability in the water column, thereby enhancing phytoplankton growth and decreasing water quality (Landers, 1982; Barko and James, 1998). Specifically, we expected to see greater increases in nutrients and chlorophyll-*a* in microcosm water that contained plants relative to control microcosms that contained sediment and lake water without plants. Due to the fast growth of the exotic weed, and more frequent defoliation (personal observation), we expected nutrients and chlorophyll-*a* differences to be more pronounced in the *M. spicatum* microcosms than in the microcosms containing *E. canadensis*.

Furthermore, water from the outdoor microcosms was filtered and added to flasks containing natural assemblages of phytoplankton in 1% and 10% concentrations. We anticipated that filtered water from plant microcosms would enhance natural phytoplankton growth in a controlled bioassay relative to filtered water from control

plants of similar size were rinsed with deionized water, and re-planted individually into darkened mason jars (175 ml). The mason jars with plants were placed into 1.5-L (44 cm tall by 7.25 cm ID) clear Plexiglas microcosm tubes (Figure 2.3). Plant roots were fed through a small hole in the center of a rubber stopper lid for the mason jars in order to separate the plant root compartment from plant shoots. We used 3M Imprint II Vinyl Polysiloxane Dental Impression Material to seal the space in the hole between the plant stem and rubber stopper in order to prevent exchange of water between the root and shoot compartments without damaging the plant stem. Plants were grown hydroponically in filtered lake water for 45 days. Root compartments of the mason jars held 135 ml of filtered lake water with a 10 μCi addition of carrier free $^{32}\text{P-PO}_3^{4-}$. Microcosm treatments consisted of one plant per tube: *M. spicatum* (^{32}P , n=10), *E. canadensis* (^{32}P , n=9), *M. spicatum* (no ^{32}P , n=10), and filtered water (no plants, no ^{32}P , n=6). There were only 9 microcosms with *E. canadensis* due to a treatment error of double ^{32}P dosage in one microcosm. All microcosms were maintained under a 14-hour photoperiod for 6 days to allow plants to acclimate and acquire ^{32}P . Each treatment was then split randomly into two groups and assigned to separate growth chambers under long (14 hr)- and short-day (10hr) photoperiods. Temperature and light levels were maintained equally in both chambers at about 18°C and 275 μmol respectively. We used three Super-Light Eco-saver compact fluorescent lamps (100 watt) per chamber.

Immediately after introduction of ^{32}P , water columns were stirred and 1-ml aliquots were sampled for liquid scintillation counting (Fig. 2.4). Additional sampling of water columns was done 36 days of the 45-day experimental period (September 9, 1999 to October 20, 1999) to monitor leakage of $^{32}\text{PO}_3^{4-}$ from plant shoots during growth and

Outdoor sediment-plant microcosms and ^{14}C phytoplankton bioassay

We established microcosms of *M. spicatum* (n=5) and *E. canadensis* (n=5) in clear, Plexiglas tubes (1.5 liters) using lake sediment from the Tahoe Keys and unfiltered lake water from Sunnyside on September 24, 1999. We included two types of controls without plants: One control consisted of lake sediment and unfiltered lake water (n=5), and the other was unfiltered lake water alone (n=4). Initial sediments and water were sampled for chlorophyll-*a* and the following nutrient analyses: $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, soluble reactive phosphorus (SRP), total phosphorus (TP) and dissolved phosphorus (DP). Microcosm tubes were maintained for five weeks outside of the Lake Tahoe Research Group Laboratory under natural photoperiod and temperature regime. Tubes were anchored in a large pool of water in randomized positions to buffer diurnal temperature flux. The tubes rose just above the surface of pool water to prevent exchange between treatments, and were covered with clear plastic bags that allowed air exchange, but prevented contamination by dust, pollen and precipitation. Water temperature, dissolved oxygen, pH, and light were measured six days after the start of the experiment in individual tubes using Yellow Springs Instruments temperature and dissolved oxygen probes and LiCor scalar irradiance (4 pi) sensor (Appendix 2.1a). Diel fluxes in temperature were measured at the end of the experiment on 10/24/99 and 10/25/99 (Appendix 2.1b). Following a five-week growth period, sediments and water were collected from individual microcosms for nutrient and chlorophyll-*a* analyses.

Samples of microcosm water columns were composited by treatment and filtered through HA Millipore® membrane filters ($0.45 \pm 0.02 \mu\text{m}$ pore size) for use in a bioassay to test the response of natural phytoplankton populations to filtered exudates from

1968). On the final day of the experiment, we measured actual chlorophyll-*a* concentrations in addition to *in vivo* fluorescence and ^{14}C -uptake radioactivity on HA Millipore membrane filters.

Decomposition

We collected *M. spicatum* and *E. canadensis* plants from the Tahoe Keys Cove East Lagoon and rinsed them three times in tap water followed by deionized water to remove epiphytes. Plants were grouped into piles of similar size, and excess water was removed by blotting with a paper towel. We measured wet weights of plants before placing them in 2mm mesh bags. Mesh bags containing plants were placed into a 60°C water bath for 1 minute to denature proteins and inhibit further plant growth. We were careful to maintain the 60°C water bath temperature because plants may lose organic compounds at higher temperatures. Plants in mesh bags were returned to the Tahoe Keys Cove East Lagoon, stapled to the lake bottom at a water depth of ~0.5m, and left to decompose. All mesh bags were placed into the lake on September 23, 1999, a natural time of senescence in the Tahoe Keys Cove East Lagoon. We harvested five mesh bags of each plant species four times over the eleven-week decomposition period, which extended into a freezing over of edges of the lagoon in December, 1999. Harvested bags were rinsed thoroughly in tap water until water ran clear, followed by three rinses in deionized water. We plucked remaining plant fragments from the mesh bags and placed the contents into a drying oven at ~60°C. Dried contents of mesh bags were weighed, ground with a mortar and pestle, and analyzed for total carbon (%-C), nitrogen (%-N) and phosphorus (%-P) nutrient analyses.

Plant nutrient contents, Total Kjeldahl Nitrogen (TKN) and the relative bioavailability of inorganic orthophosphate (Olsen-P) in lake sediments were determined by the Division of Agriculture and Natural Resources (DANR) Analytical Laboratory at UC Davis. Methods for plant nutrient contents were identical to those described in Chapter 1. The TKN of sediment was determined by the wet oxidation of soil organic matter using the standard Kjeldahl procedure with sulfuric acid and digestion catalyst (Isaac and Johnson, 1976; Carlson, 1978). The method for extractable phosphorus followed that developed by Olsen et al. (1954), Olsen and Sommers (1982) except that ascorbic acid was substituted for stannous chloride.

Statistical Analyses

Cycling of ^{32}P in hydroponic aquatic plant microcosms

We calculated initial activities, A_0 (μCi), from the activities remaining, A , after time t generated through liquid scintillation counting, considering the 14.3 day half life of ^{32}P over the course of the experiment ($A_0 = A/e^{-(\ln 2/14.3)t}$). Activities were converted to disintegrations per minute (dpm) ($1 \mu\text{Ci} = 2.2 \times 10^6 \text{ dpm}$). We normalized activities in plant tissues by dividing by dry weights of plants. In three instances, there was insufficient plant material to get an accurate reading, thus these points were left out of the analysis (Appendix 2.2).

We used a three-factor Analysis of Variance (ANOVA) with repeated measures and interactions to determine the effects of *M. spicatum* and *E. canadensis* under long- and short-day photoperiods on ^{32}P activities in microcosm water columns. We determined ^{32}P release rates according to the slope of the lines for activity over time in the water of microcosms of *M. spicatum* and *E. canadensis*. The same ANOVA model

differences in $\text{NO}_3\text{-N}$ among treatments in the water of microcosms with and without plants.

Using a two-way repeated measures ANOVA, we tested the effect of repeated measurements in the bioassay flasks on *in vivo* and ^{14}C -uptake responses of phytoplankton growth. Simple 2-way ANOVA's with (conservative) Bonferroni pairwise comparisons determined differences *in vivo* and ^{14}C -uptake responses to bioassay treatments over time.

Under the assumption that flasks had no effect on chlorophyll-*a* concentrations in this experiment, one-way ANOVA was used to determine differences in the actual chlorophyll-*a* concentrations on the final day of the bioassay due to the plant, sediment, and control water treatments. Given that repeated measures of the *in vivo* chlorophyll-*a* growth response was not a significant source of variation in the bioassay, this assumption seems valid for actual chlorophyll-*a* response. Tukey-Kramer HSD and Bonferroni pairwise comparisons revealed significant differences between specific treatment pairs.

Decomposition

A *ln*-transformation of the %-remaining response in a two-way ANOVA was utilized to determine the effects of removal date and plant species on decomposition. We assessed differences in %-C, %-N, and C/P-ratio of mesh bags according to removal date and plant species without transformations using two-way ANOVA. In the same two-way ANOVA model, we used *ln*-transformations of %-P, C/N, and C/P in order to ensure normal distribution of residuals.

The amount of ^{32}P activity remaining in the root compartments (mason jars) of the microcosms differed by sampling date, plant species, and photoperiod (ANOVA, $F = 28.901_{23,32}$, $p < .0001$) (Fig. 2.8, Table 2.2a). According to this analysis, ^{32}P activity in the hydroponic solution in root compartments was greater, on average, for short-day microcosms than long-day microcosms only on the mid-experiment sampling date, September 15, 1999 ($t = 4.162$, $p = .0002$) (Table 2.2b). The hydroponic solution in root compartments with *M. spicatum* plants had higher levels of ^{32}P activity on average than those of *E. canadensis*, implying that *E. canadensis* took up more ^{32}P . However, this difference was significant only on September 15, 1999 (Bonferroni, $t = 3.613$, $p = .0010$). The replicate, MS5 (long-days), was excluded from the analysis for October 20, 2000 due to a sampling error on this date. Residuals of the model were normally distributed (Shapiro-Wilk, $W = 0.9631$, $p = .1704$).

Figure 2.9 illustrates mean ^{32}P activities in the various biological and abiotic microcosm compartments. ^{32}P in the hydroponic solution of root compartments was by far the dominant reservoir of ^{32}P activities on the final day of the experiment, and is shown for comparison in Figure 2.10. Suspended particulate matter (SPM) in 20-ml of water from microcosms was collected on filters prior to acid digestion. Biofilm (wall) on side walls of the microcosms were also included in this analysis. Plant parts of MS and EC included roots, shoots, leaflets that had fallen off shoots prior to the final day, and green-apical meristems (3-4cm). This budget also takes into account the extraction of 10-ml of water containing activity from root compartments on 09/15/99. Microcosm EC2 and should be excluded from this figure, as it has been from the statistical analysis because it received a double dose of ^{32}P activity at the beginning of the experiment. It

Residuals of the model using the \ln -transformed dry weights were normally distributed (Shapiro-Wilk, $W = 0.946$, $p = .3417$). Final biomass of shoots, measured by dry weight, were not affected by photoperiod. Because we did not measure initial biomass, we cannot compare changes in productivity over the growth period.

We found that root biomass differed by photoperiod, but not according to plant species ($F = 10.780_{1,17}$, $p = 0.0044$). Plant roots grown under long-day photoperiods had a greater biomass than plant roots under the short-day treatment. Mean root biomass for *M. spicatum* plants grown under long-days was (0.0094 ± 0.0032 g) and (0.0019 ± 0.0026 g) for short-day length plants. For *E. canadensis*, mean root biomass for the long-day photoperiod was (0.0121 ± 0.0087 g), and (0.0342 ± 0.0451 g) for the short-day treatment. Residuals of the model using weighted regression and transformation (transformation = $\ln(\text{dry weight} + 0.0001)$) were normally distributed (Shapiro-Wilk, $W = .9190$, $p = .1120$). Although initial root biomass was not measured, plants of apparent equal size and health had been chosen and randomly assigned to photoperiod treatments.

The sample size ($n=5$) was insufficient to distinguish effects of photoperiod on the production (dry weight) of green apical meristems or in leaflets shed from shoots.

We constructed a budget of ^{32}P activity measured in the various biological and abiotic components of the microcosms on October 20, 1999 to account for the flow of ^{32}P from sealed root compartments over the 45-day experimental period (Fig. 2.10). This budget suggests that by the final day of the experiment most of the ^{32}P activity had returned to the water of the root compartment. A fair amount of activity was also present in plant roots and green apical meristems.

there was not enough replication to determine statistical differences. Mean DP concentrations in treatments were: Initial lake water = 5.0 ± 0.0 ppb, *M. spicatum* = 12.4 ± 7.8 ppb, *E. canadensis* = 7.8 ± 5.2 ppb, sediment = 5.2 ± 0.8 ppb, and lake water = 5.5 ± 1.9 ppb.

Similarly, $\text{NH}_4\text{-N}$ and SRP appeared to be on average higher in the water of microcosms with *M. spicatum* ($\text{NH}_4\text{-N} = 12 \pm 8.6$ ppb, SRP = 4 ± 1.2 ppb) and *E. canadensis* ($\text{NH}_4\text{-N} = 19 \pm 40.3$ ppb, SRP = 3.8 ± 03.5 ppb) than in control microcosms with sediments ($\text{NH}_4\text{-N} = 6.2 \pm 10.5$ ppb, SRP = 2.0 ± 0.0 ppb) and lake water ($\text{NH}_4\text{-N} = 8.3 \pm 14.6$ ppb, SRP = 2.3 ± 0.5 ppb) (Figs. 2.16, 2.17). However, variation in nutrient concentration within treatments was too high to detect differences with the small sample sizes ($n=5$) of this experiment.

Although sample sizes were too small to establish differences due to treatment in TKN or Olsen-P in microcosm sediments after the 5-week growth period, patterns of mean TKN between treatments support the hypothesis that sediments in plant microcosms would be depleted in nutrients relative to the no-plant controls. Mean values for TKN and Olsen-P are given in Table 2.4. Individual measurements of all nutrients and chlorophyll-*a* are given in Appendix 2.4.

In the six-day ^{14}C bioassay using natural lake phytoplankton, *in vivo* chlorophyll-*a* varied according treatments, dates, and the interaction, treatment*date (ANOVA, $F = 44.377_{29,51}$, $p < .0001$) (Table 2.5a). *In vivo* fluorescence increased over the six day period in all flasks, but to the greatest extent in treatments of *M. spicatum*. (Fig. 2.18). Residuals of the model were normally distributed (Shapiro-Wilk, $W = 0.965$, $p = .1052$).

Actual chlorophyll-*a* concentrations measured on the final day of the bioassay varied by treatment (ANOVA, $F = 6.439_{9,16}$, $p = .0007$). Residuals were normally distributed (Shapiro-Wilk, $W = 0.969$, $p = .6049$). However, Tukey-Kramer HSD pairwise comparison revealed that all the variation was due to the DI 1% treatment, which yielded significantly lower chlorophyll-*a* concentrations than the other treatments. When this parameter was removed from the analysis, data remained normally distributed (Shapiro-Wilk, $W = 0.973$, $p = .7125$), and bioassay treatments no longer had an effect on actual chlorophyll-*a* concentrations (ANOVA, $F = 2.172_{8,16}$, $p = .0888$).

Decomposition

The proportion of material remaining in mesh bags after decomposition differed based on the date of removal from the lake, plant species, and the interaction between these two factors (ANOVA, $F = 34.325_{9,37}$, $p < .0001$) (Table 2.7a). There was a general decrease in the amount of material remaining in mesh bags over time, and bags containing *E. canadensis* lost on average, 8% more material than bags containing *M. spicatum* (Table 2.7b). We fit exponential decay curves to the data for % remaining after decomposition and found that the decay constant for *E. canadensis* ($r = 0.0275$) was greater than *M. spicatum* ($r = 0.0109$). (Fig. 2.20). Decomposition of *E. canadensis* ($R^2 = 98\%$) followed an exponential decay pattern more closely than *M. spicatum* ($R^2 = 94\%$). Individual dry weights of mesh bags containing *M. spicatum* and *E. canadensis*. are given in Appendix 2.5. With a \ln -transformation, residuals of the model were normally distributed (Shapiro-Wilk, $W = .9596$, $p = .1704$).

all dates after the control subset (September 23, 1999), as indicated by negative parameter estimates for all dates (Table 2.10b). This difference was marginally significant on November 17, 1999 ($p=.0712$). Although as a main effect, plant species was not significant as a main effect, the total %P was different in *M. spicatum* vs. *E. canadensis* on particular dates of harvest. In the initial control mesh bags, phosphorus was significantly greater in *E. canadensis* than *M. spicatum*, and marginally so after 2 weeks of decomposition ($p = .0780$). Data were *ln*-transformed so that residuals met the normal distribution requirement of ANOVA (Shapiro-Wilk, $W=.9931$, $p=.9973$).

Mean C/N ratios were 14.78 ± 0.79 for *M. spicatum* and 17.27 ± 1.39 for *E. canadensis* at the start of the decomposition experiment. During the 11-week decomposition period, the C/N ratio differed in decomposition bags according to the date of removal and plant species ($F = 11.316_{5,41}$, $p<.0001$) (Fig. 2.22, Table 2.11a). On average, C/N was greater by 0.09 in bags containing *E. canadensis* than *M. spicatum* (Table 2.11b). The C/N ratio was lower in bags after 1 month (October 23, 1999) and 2 months (November 17, 1999) than the original control groups (September 23, 1999), but was higher at the end of the 11-week decomposition period (December 5, 1999). Natural log-transformed data were normally distributed (Shapiro-Wilk, $W=.995$, $p=.1122$).

Initial C/P ratios of *M. spicatum* and *E. canadensis* were 157.63 ± 48.06 and 97.60 ± 10.48 respectively. During the course of the experiment, C/P ratios of mesh bag contents were affected by removal date and the interaction of date and plant species (ANOVA, $F=15.501_{9,37}$, $p<.0001$) (Fig. 2.22). C/P ratios increased with time across all removal dates. Data were *ln*-transformed and residuals of the model were normally

September 15, 1999, suggesting greater uptake of ^{32}P by *E. canadensis* plants (Fig. 2.4).

The greater biomass of *E. canadensis* photosynthetic shoots also implies a greater demand for uptake of ^{32}P relative to *M. spicatum* (Table 2.4). Despite the greater capacity of *E. canadensis* to acquire ^{32}P in its tissues, release of ^{32}P into the water columns was nine times as great in microcosms with *M. spicatum* than microcosms with *E. canadensis* (Fig. 2.5). Acquisition of ^{32}P by suspended phytoplankton, bacterioplankton and detritus (SPM) also appeared to be greater in microcosms containing *M. spicatum* than *E. canadensis* (Figure 2.6). These results suggest that regardless of photoperiod, the invasive macrophyte, *M. spicatum*, releases phosphorus into the water column during growth and senescence to a greater extent than the native plant, *E. canadensis*, thereby contributing to a decrease in Lake Tahoe water quality. *

The intent of long- and short-day photoperiods was to induce senescence in plants under short-daylengths; however, plants of both species showed signs of senescence equally in both treatments (Figures photographs a-d). Thus, photoperiod did not appear to effect differences in senescence or in the amount of ^{32}P leaked by *M. spicatum* and *E. canadensis* into microcosm water columns. It is possible that a more intense senescence of plants under short photoperiods would have occurred if we reduced temperatures in that growth chamber. Although the final biomasses of shoots did not differ between photoperiod treatments, we cannot draw conclusions about differences in productivity during the experimental period because we did not make initial biomass measurements.

Because phosphorus leakage from *M. spicatum* was concurrent with senescence of some plant shoots, we were unable to distinguish between ^{32}P released from senescent shoots vs. healthy shoots. However, in a similar experiment isolating roots and shoots,

exalbescens, and Smith and Adams (1986) determined that shoot turnover was responsible for the release of $2.8 \text{ g P m}^{-2} \text{ yr}^{-1}$ in Lake Wingra. It is also possible that higher levels of ^{32}P released to water in *M. spicatum* microcosms was related to higher levels of defoliation by this species than by *E. canadensis*. Not enough leaf litter was produced by *E. canadensis* in this study to obtain dry weights or ^{32}P activity data. More intense defoliation by *M. spicatum* than *E. canadensis* is evident by numerous shed leaflets in Figures 2.5a and 2.5b.

Carignan and Kalff (1982) found that epiphytes on plant tissues derived only 3.4-9.0% of their P from *M. spicatum* grown *in situ*. Due to the adhesive nature of epiphytes and biofilm on plant tissues, it was not possible to achieve separate measurements of ^{32}P in these biological compartments of this microcosm study. However, the low counts of ^{32}P in suspended particulate matter and biofilm growing on the Plexiglas microcosm walls (Table 2.3) suggests that small amounts of leaked ^{32}P may have been absorbed by epiphytes and phytoplankton.

The fact that the total activity presented in the budget on October 20, 1999 falls short of the original activity introduced to the sealed root compartments on September 4, 1999 may be explained by a minor loss of activity in the daily 1-ml sampling regime of the water column. Other discrepancies may be due to tiny plant fragments in the root compartment and water column that we could not easily collect at the end of the experiment. Finally, a substantial biofilm that contained ^{32}P activity (data not presented) had collected on the surfaces of the rubber root seals. Unfortunately, these stoppers were not rigorously sampled for this analysis.

Given that there were no differences in actual chlorophyll-*a* concentrations among the bioassay treatments on the final day of the experiment, this phytoplankton growth response does not appear to be as sensitive to the plant, sediment, and control water treatments as the *in vivo* fluorescence and ^{14}C -uptake responses of phytoplankton growth.

Decomposition.

In their study of decomposition among six aquatic plants, Twilley et al. (1986) determined that decomposition rates were directly proportional to the initial nitrogen content in plant tissues. In this on study we found that decay of *E. canadensis* occurred faster than *M. spicatum*, despite higher concentrations of nitrogen in *M. spicatum*. Initial N and P in plants taken from the Tahoe Keys for the decomposition experiment (*M. spicatum* = 2.78% N, 0.28% P; *E. canadensis* = 2.09% N, 0.37%P) were greater than the minimum tissue content of 1.3% N and 0.13% P associated with maximum growth of aquatic plants suggested by Gerloff and Krombholz (1966). These values were similar to those of *Myriophyllum* spp. collected from the highly fertile Lake Mendota were 2.63%N and 0.38% P (Gerloff and Krombholz, 1966), and imply that decomposition should not have been limited by either element (Nichols and Keeney, 1973).

Graneli and Solander (1988) claim that relative resistance of litter to decomposition results from high structural carbohydrate content and low nutrient content. We propose, however, that production of antimetabolites in macrophytes may also influence rates of decomposition. Gross et al. 1996 isolated algaecidal, hydrolysable polyphenols from *M. spicatum* that inhibited the growth of phytoplankton and reduced competition for light. It is possible that high concentrations of phenolic compounds,

bag contents in the decomposition experiment suggest that C/N was greater in decay materials of *E. canadensis* than *M. spicatum*. Since *E. canadensis* decomposed faster than *M. spicatum*, we would have expected lower C/N in the contents of *E. canadensis* mesh bags. Similarly, C/P ratios were lower in the contents of mesh bags containing *M. spicatum* than those with *E. canadensis*. Either more microbes with lower C/P ratios colonized mesh bags with *M. spicatum*, or phosphorus was more readily lost from mesh bags containing *E. canadensis*. We propose that although *M. spicatum* has higher N and P concentrations, and therefore is more nutritious, it decomposes less readily because it may produce more secondary compounds than *E. canadensis*.

The C/N ratio was lower in decay materials after 1 month (October 23, 1999) and 2 months (November 17, 1999) than the original control groups (September 23, 1999), but was higher at the end of the 11-week decomposition period (December 5, 1999). This seems contrary to our expectation that C/N would decrease over time as mesh bags are colonized by decomposers with lower C/N ratios. We found that C/P ratios in mesh bags also increased with time across all removal dates, contradicting the expectation that colonization of mesh bags by decomposers with lower C/P ratios would cause a net decrease in C/P ratios of mesh bags over time.

Despite the abundant nitrogen contents of plants (*M. spicatum* = 2.78% N, *E. canadensis* = 2.09% N), low N/P ratios of 10.66 for *M. spicatum* and 5.69 for *E. canadensis* suggest, nitrogen would be a more limiting element to plant growth than phosphorus. Results of this study suggest that on average the N/P ratios were greater in bags containing *M. spicatum* than in bags with *E. canadensis*, implying that either *M. spicatum* was enriched in N or depleted in P relative to *E. canadensis*. In general, the

macrophytes at Lake Tahoe. Again, stable isotopes and radioactive tracers could help distinguish pathways of nutrient cycling in this complex system of decomposition. Because metabolic activity and the availability of nutrients are tightly coupled to temperature and redox conditions in sediment and water (Nichols and Keeney, 1973, Schlesinger, 1997), future studies in the Tahoe Keys and other Lake Tahoe sites should consider these parameters as well. Analysis of plant tissues for antimetabolites, together with microbial bioassays, may explain differences in decomposition between *M. spicatum* and *E. canadensis*.

Conclusions

In summary, more phosphorus than nitrogen was released from decomposing macrophytes in the decomposition study. Despite higher N concentrations in *M. spicatum*, *E. canadensis* decomposed faster in the fall of 1999. Based on previous studies of antimetabolite production by *M. spicatum* (Gross, 1995; Gross et al., 1996), we propose that *M. spicatum* may contain higher levels of secondary compounds that deter decay by microbes.

Results of the ^{32}P hydroponic plant microcosms, sediment-plant microcosms and ^{14}C bioassay seem to concur. More ^{32}P was leaked from *M. spicatum* shoots than from *E. canadensis* in growing and senescing plants. Rørslett et al. (1986) reported that no major nutrient enrichment of lake water occurred in Lake Steinsfjord, Norway, as a result of an *E. canadensis* invasion, except during a few short-term die-back periods. Most of the phosphorus taken up by *E. canadensis* is internally cycled between generations (Graneli and Solander, 1988). It is possible, that physiologically, *E. canadensis* internally cycles

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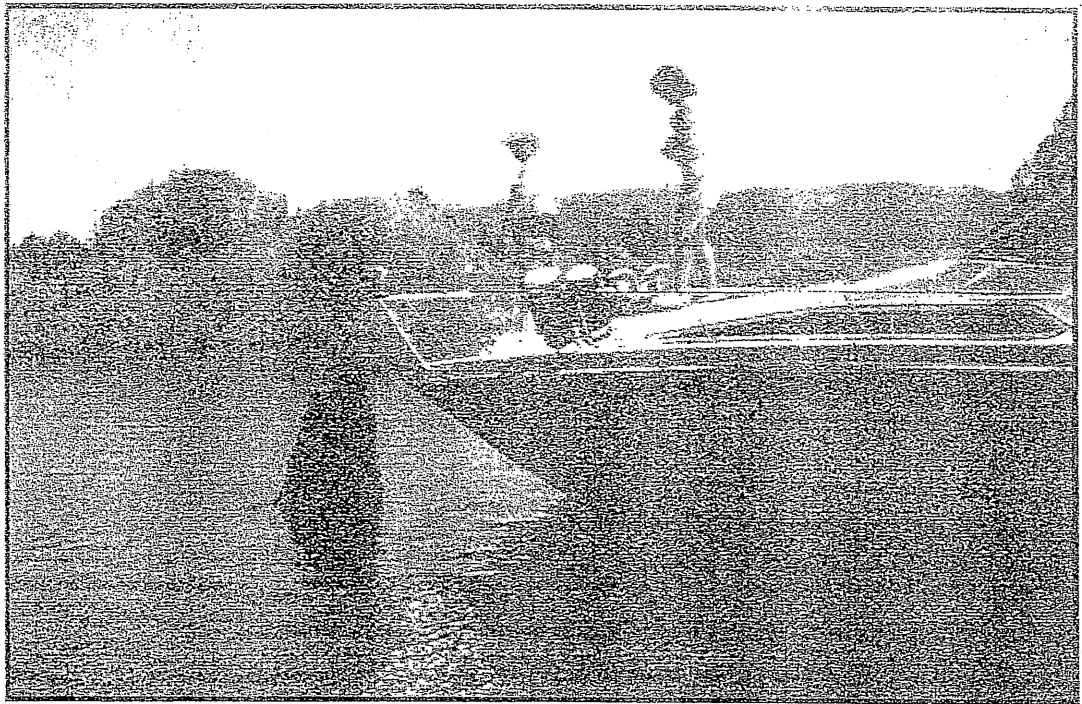


Figure 1.1 Top: *Myriophyllum spicatum* caught on a boat motor in the Tahoe Keys Cove East Lagoon, Lake Tahoe. Bottom: Mechanical harvesting of *Myriophyllum spicatum* in recreational area of the Tahoe Keys Marina, Lake Tahoe.

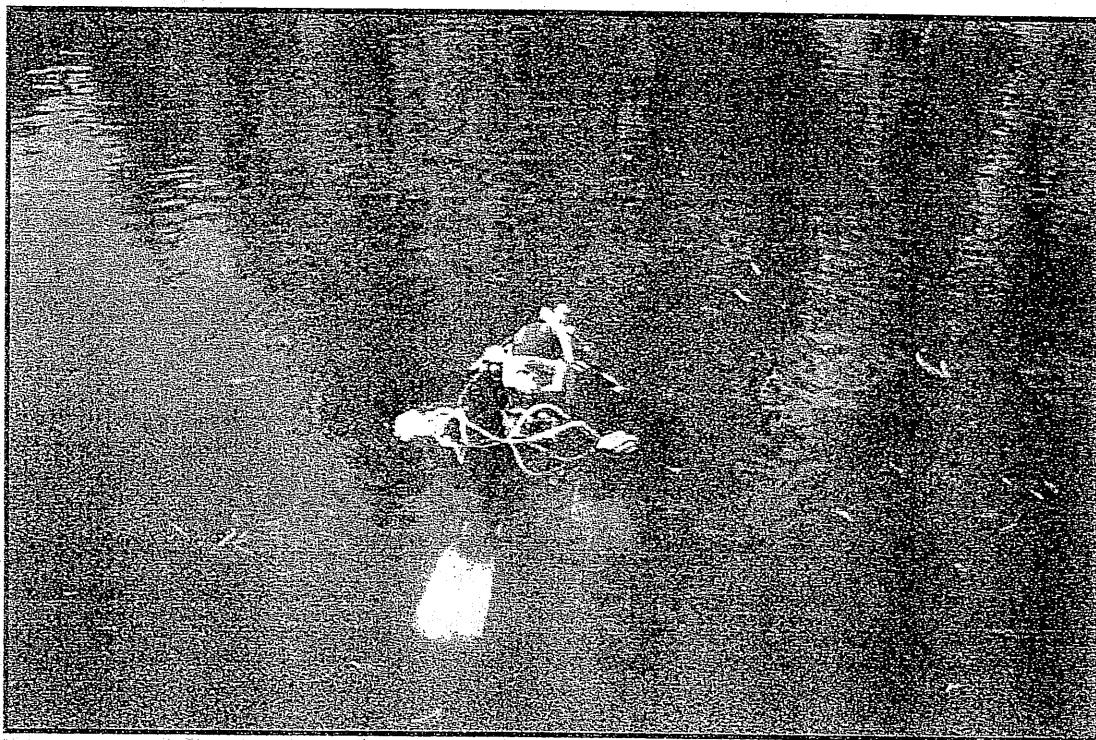


Figure 1.3. Fragments of *Myriophyllum spicatum* floating in Meeks Bay Marina represent the vegetative reproductive process, autofragmentation, which facilitates the spread of this species.

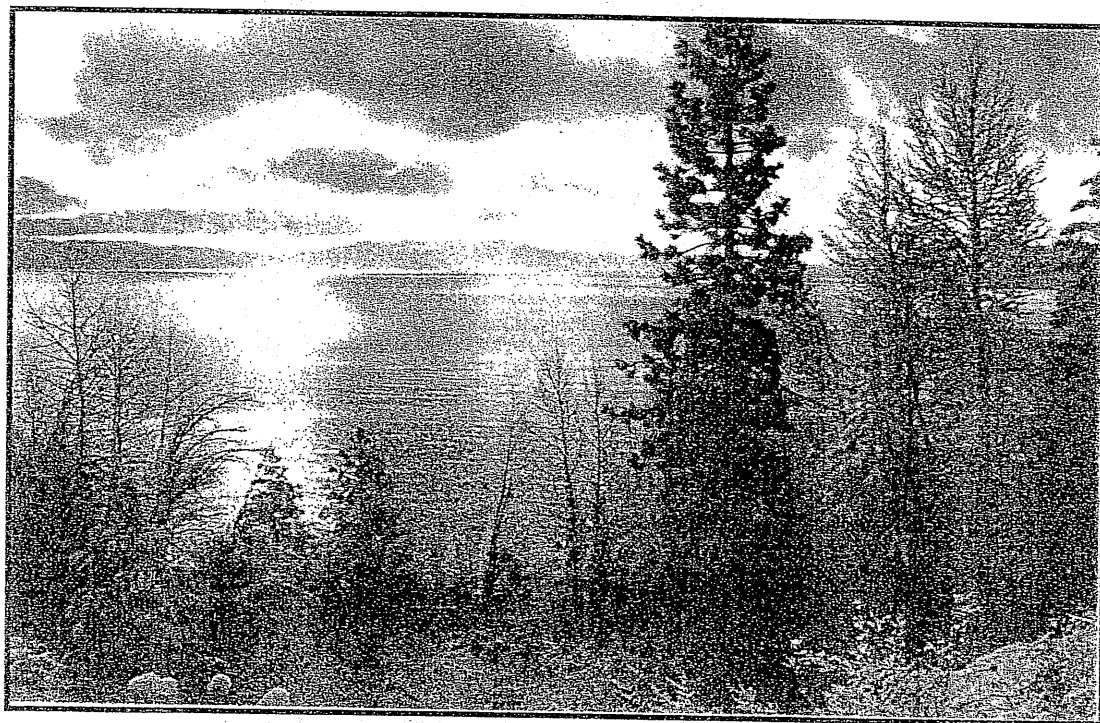


Figure 1.5. Ultra-oligotrophic subalpine Lake Tahoe, California-Nevada.

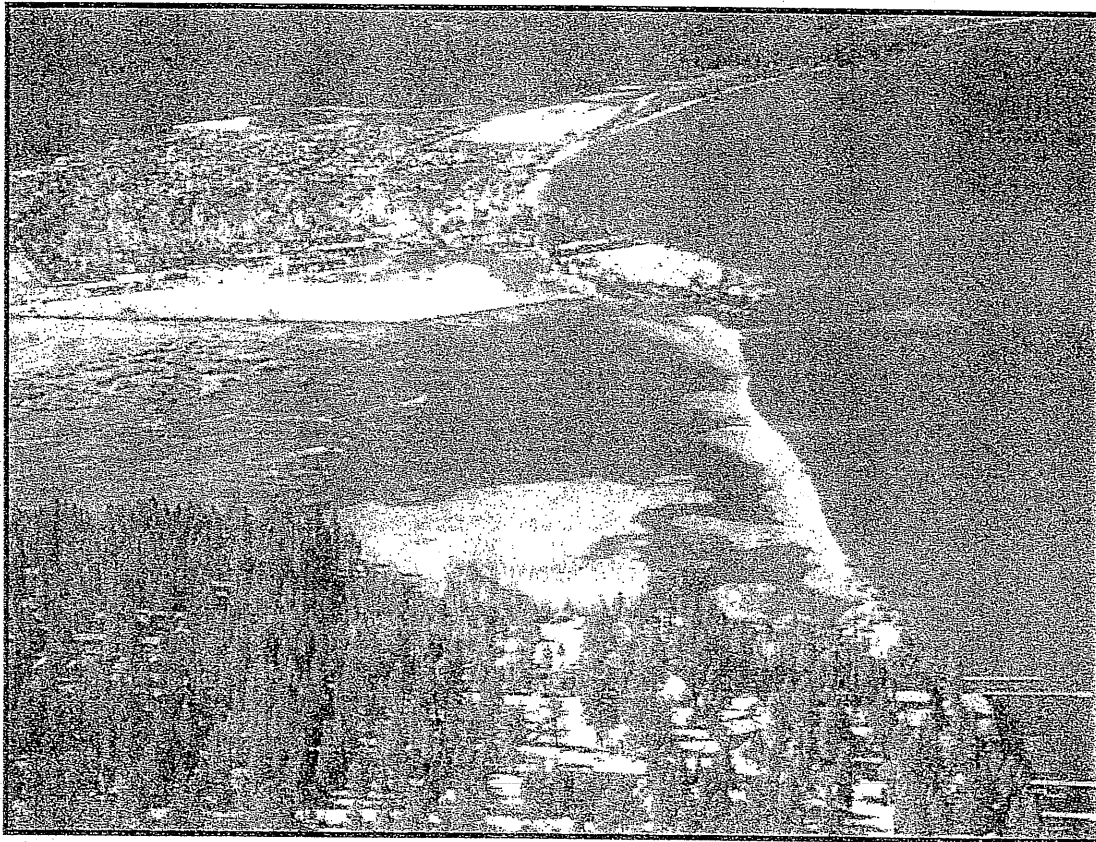


Figure 1.7. The Tahoe Keys Marina (south shore) supports the greatest growth of *Myriophyllum spicatum* at Lake Tahoe, and lies between Pope Marsh and the Upper Truckee River delta. Tahoe Keys East Cove Lagoon was a common site of study in this project.

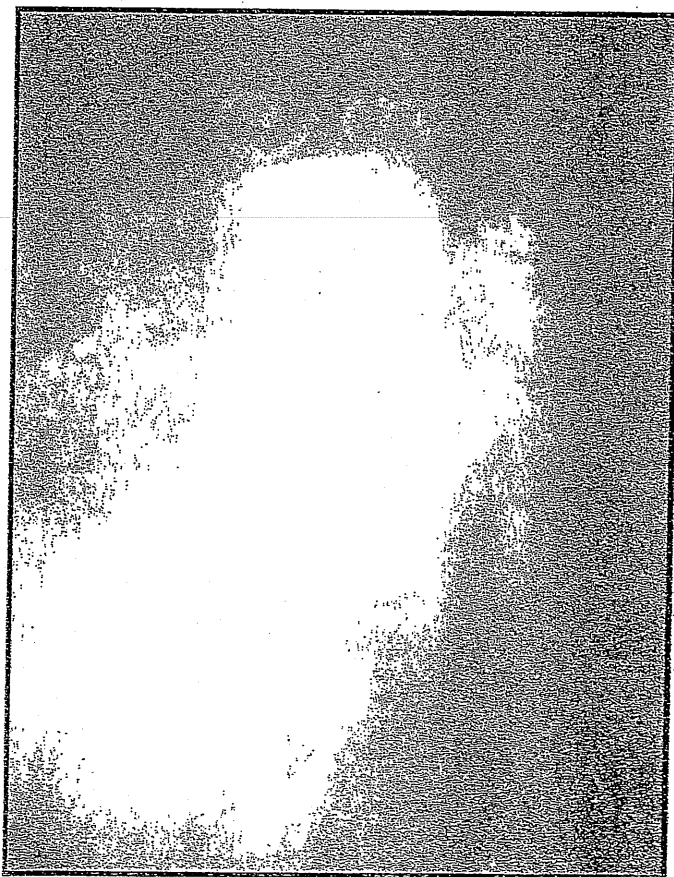


Figure 1.12. Top: sampling interstitial sediment pore water from transplant containers with *Myriophyllum spicatum* on the final day of the experiment. Bottom: *In situ* growth of *Myriophyllum spicatum* in plastic buckets under reciprocal transplant treatments of sediment source and transplant site.

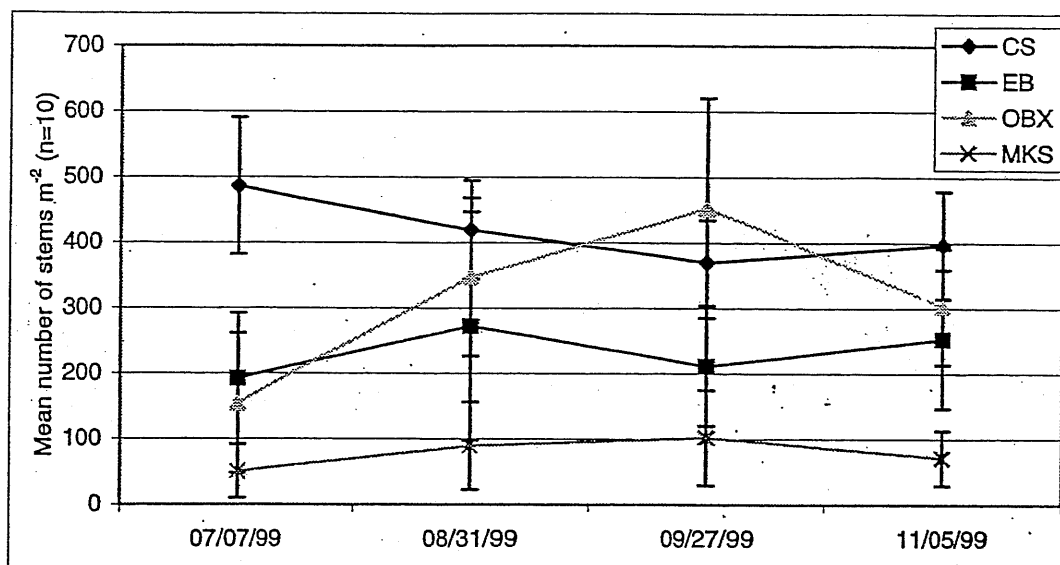


Figure 1.14 . Changes in mean density of *M. spicatum* at four Lake Tahoe locations over Summer 1999: Crystal Bay Marina (CS), Emerald Bay (EB), Obexer's Marina (OBX), and Meeks Bay Marina (MKS). Differences by site, date, and sampling point along transects were significant ($F = 27.964_{53,104}$, $p < .0001$). Data were transformed in statistical analysis to meet ANOVA assumptions of normality, but are presented in raw form here.

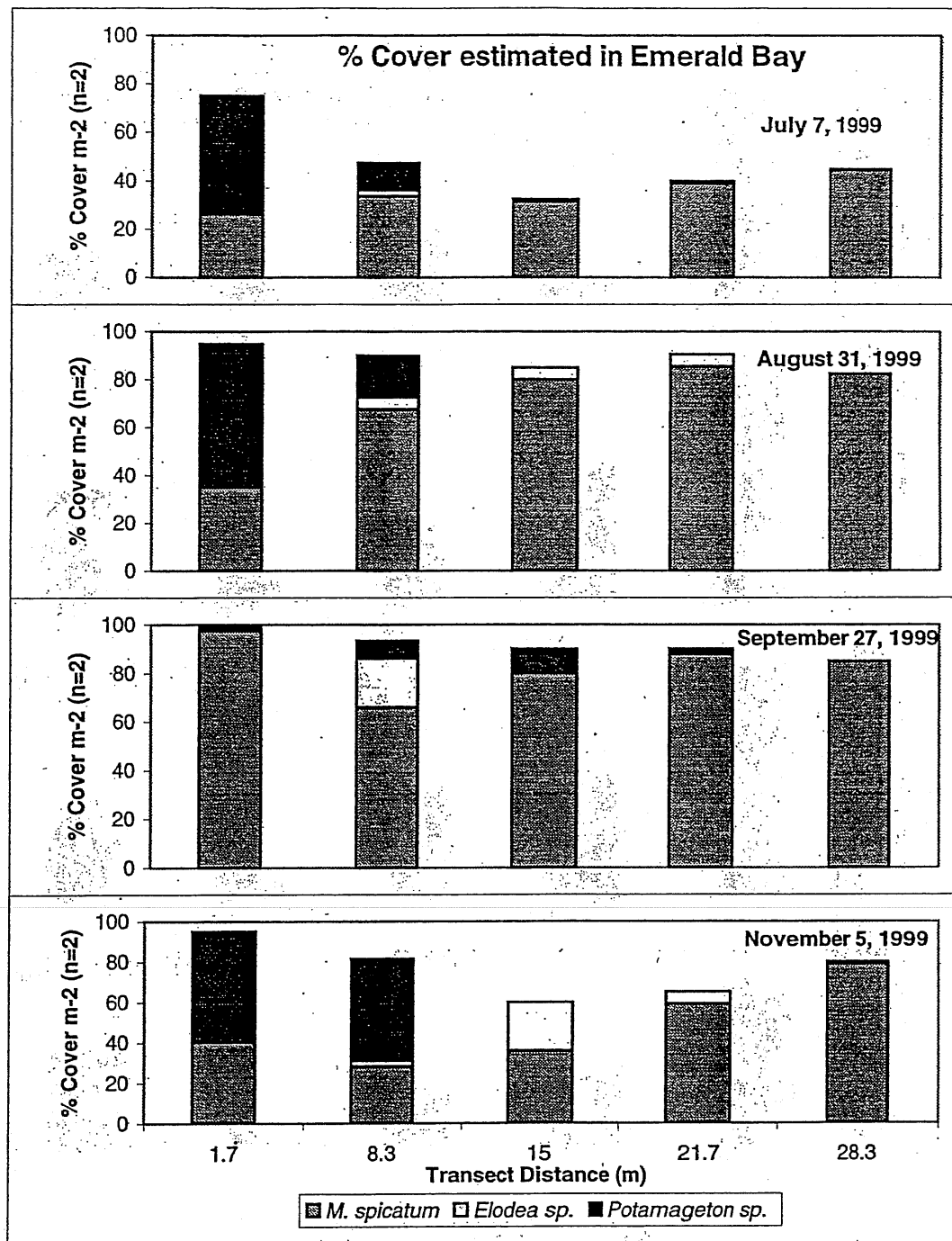


Figure 1.16a. The estimated percent cover of *M. spicatum* at Emerald Bay increased from July 7, 1999 to September 27, 1999, displacing other native macrophytes. By November 5, 1999 the percent cover of *M. spicatum* decreased and that of native plants increased.

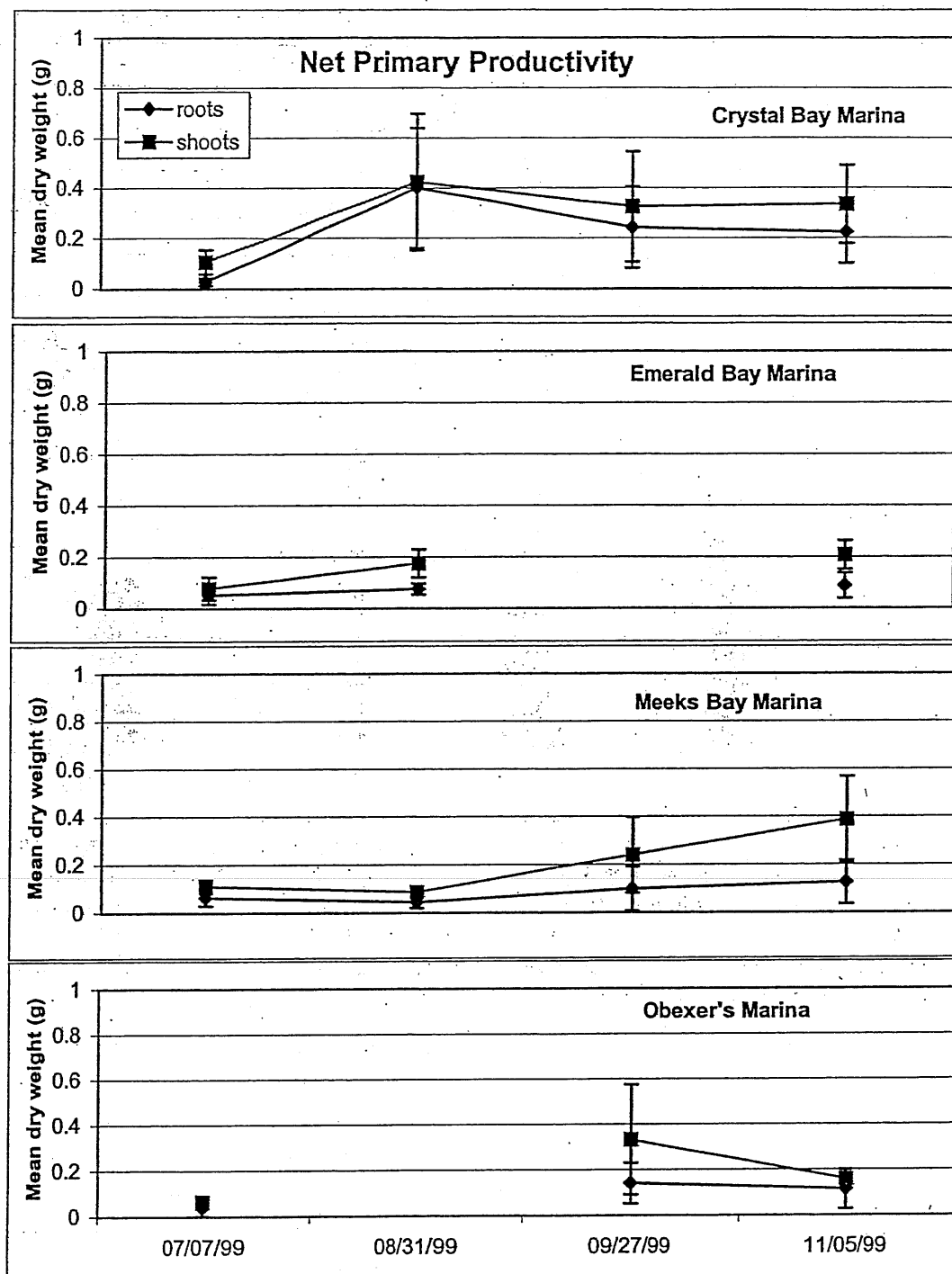


Figure 1.17a. Net primary productivity (NPP- mean biomass) of *M. spicatum* increased from July 7, 1999 through September 27, 1999. It decreased slightly by November 5, 1999. Plant biomass was greater, on average, at Crystal Bay marina than at the other sites. Differences biomass of roots and shoots were significant according to survey site and date (ANOVA, $F = 13.048_{14,121}$, $p < .0001$). On the August sampling date, Meeks Bay had six sampling points ($n=6$), and on the September date it had only three ($n=3$).

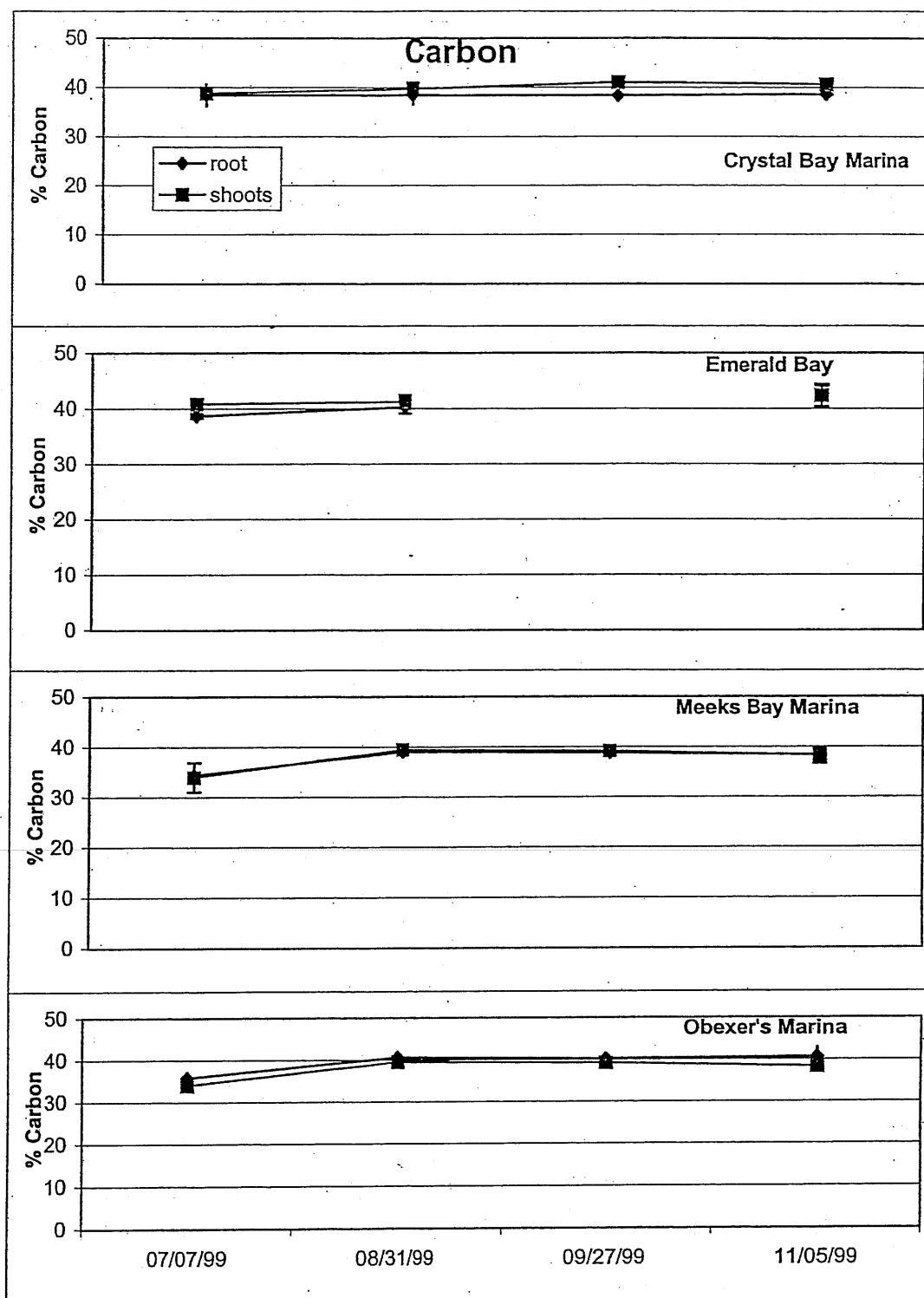


Figure 1.18a. Total %C of *M. spicatum* plants varied according to the Site*Date interaction and root and shoot plant parts, and the 3-way interaction of Site*Date*root/shoot ($F = 11.443_{29,112}$, $p < .0001$). Carbon seems to increase slightly over the summer at all four sites. Shoot carbon is slightly higher than root carbon except at Obexer's Marina. Missing points are the result of inadequate plant biomass for nutrient analyses.

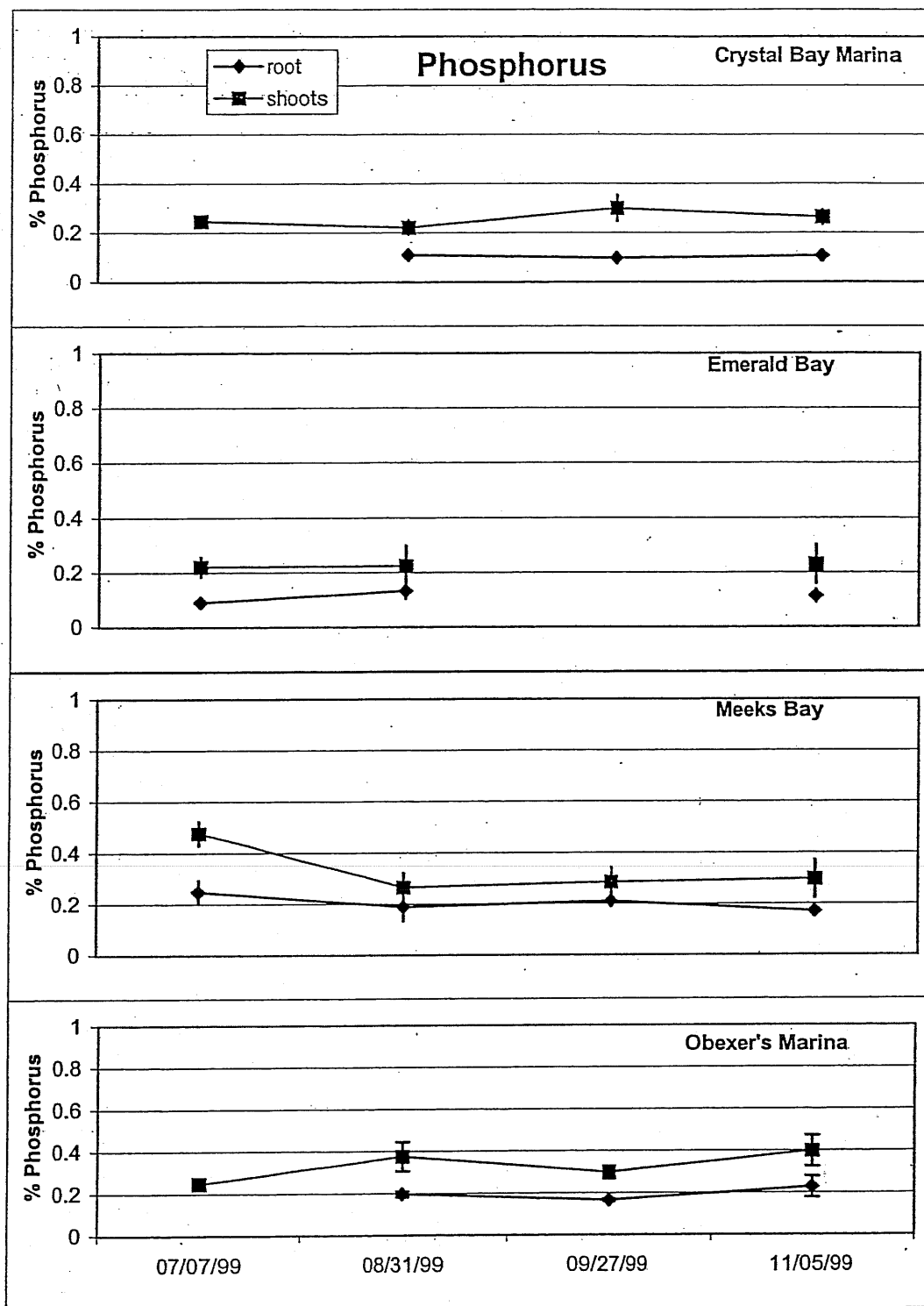


Figure 1.18c. Total %P of *M. spicatum* plants varied according to the site*date interaction and root and shoot plant parts ($F = 3.483_{15,110}$, $p < .0001$). For P, roots are always higher than shoots. There is no obvious trend in % P data any of the sites over the summer, except, at Meeks Bay where P appears to have decreased with time. Missing points are the result of inadequate plant biomass for nutrient analyses.

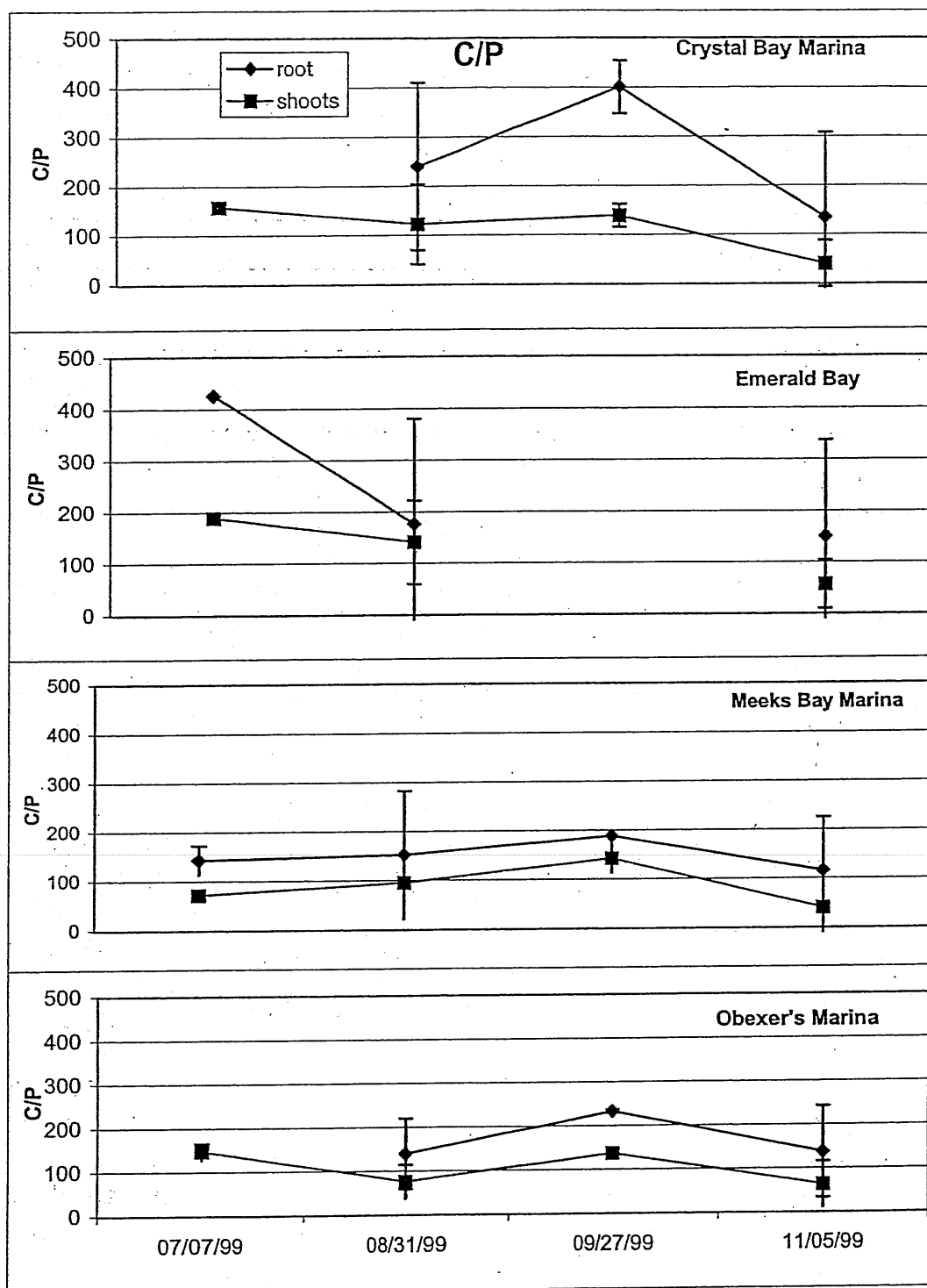


Figure 1.19b. Ratios of C/P in *M. spicatum* plants varied by Site*Date concatenations and root vs. shoot plant parts (ANOVA, $F = 3.48_{15,110}$, $p < .0001$). C/P appears to increase until September 27, 1999, and then by November 5, 1999, the C/P ratio has fallen substantially. This means that by the end of the summer roots and shoots have become more P rich. In all cases, shoots have a lower C/P ratio, suggesting that they are more P rich than roots. Missing points are the result of inadequate plant biomass for nutrient analyses.

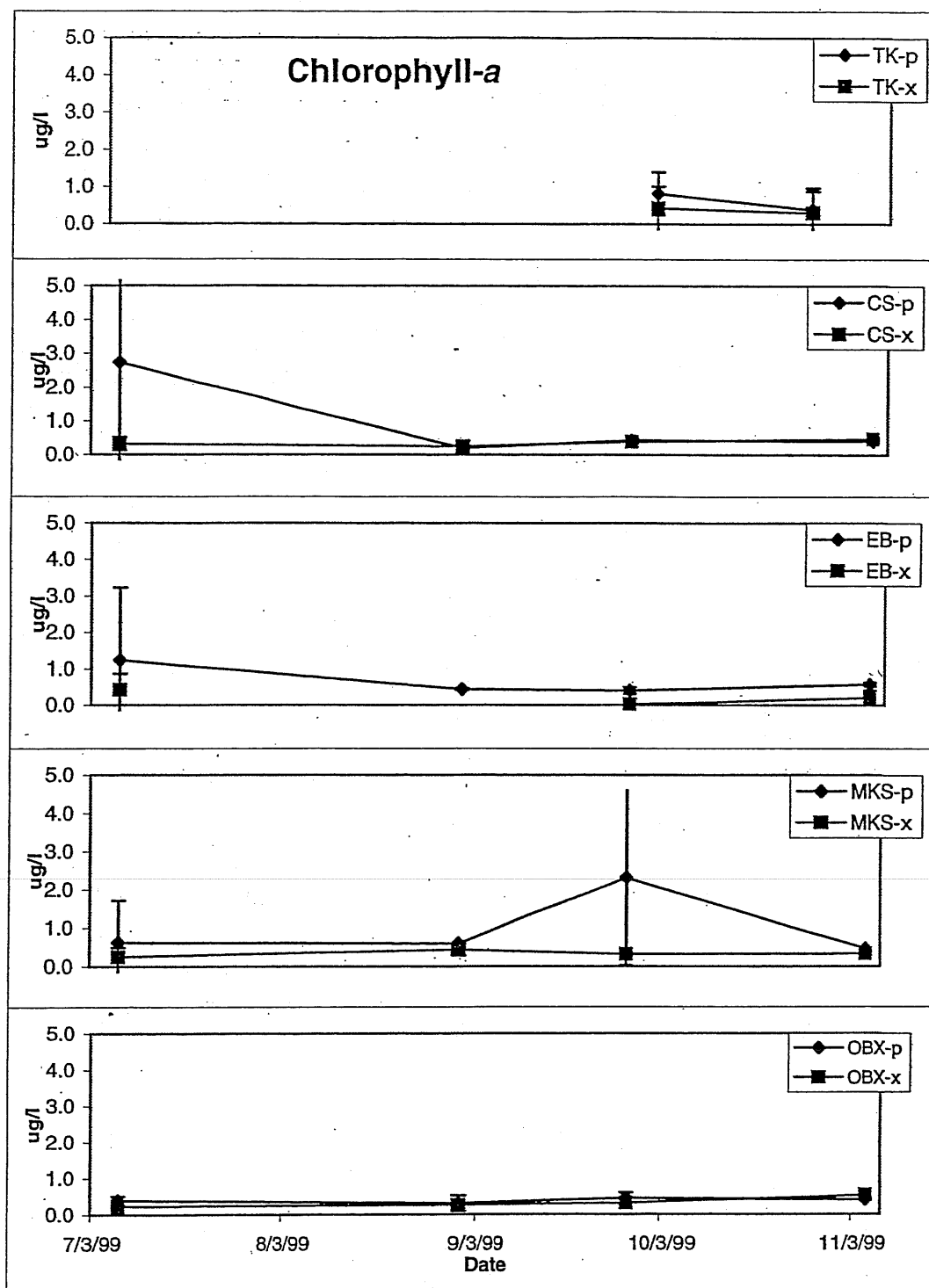


Figure 1.20. Mean chlorophyll-a in lake water on four dates in Summer 1999 in areas with (p) and without plants (x) from the Tahoe Keys (TK) and four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). The ranking of chlorophyll-a in an extension of Kruskal-Wallis differed according to survey date, site, and the presence or absence of *M. spicatum* plants at sites ($F = 8.972_{23,136}$, $p < .0001$).

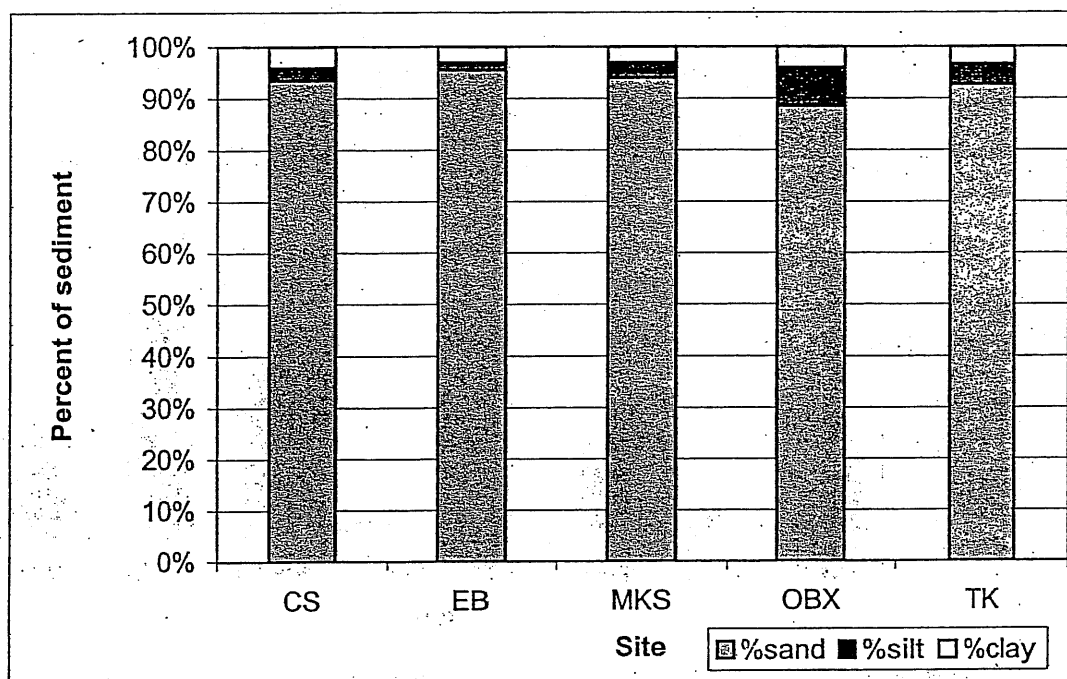


Figure 1.22. Particle size distribution of sediment from the Tahoe Keys East Cove Lagoon (TK), and four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Because sample sizes were small ($n=2$ or 3), we did not detect differences in particle size according to site, date, or the presence or absence of plants.

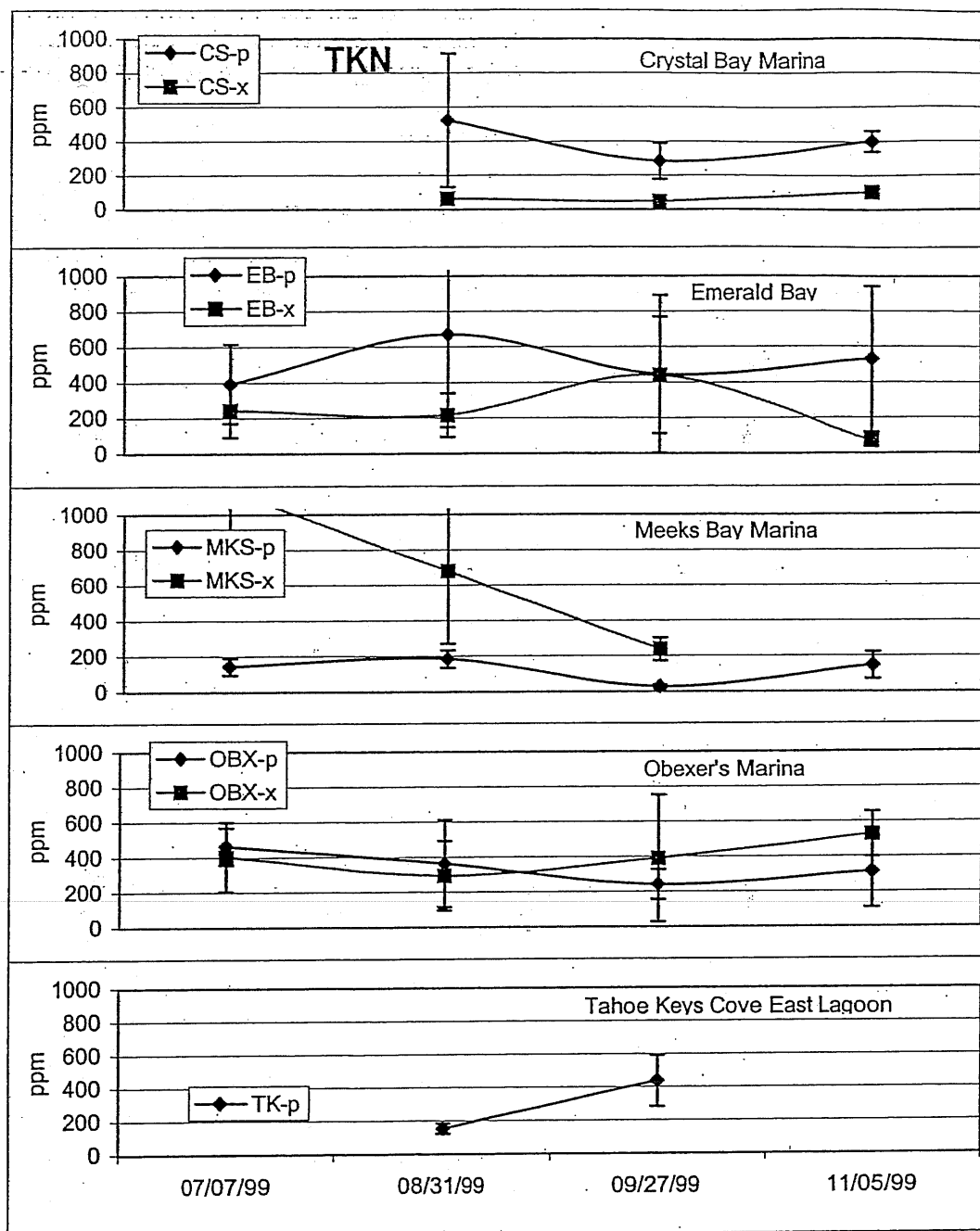


Figure 1.24. Total Kjeldahl nitrogen (TKN) in sediments supporting *M. spicatum* plants (p) and sediments without plants (x) at four Lake Tahoe survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Mean TKN from the Tahoe Keys East Cove Lagoon (TK), the largest source of *M. spicatum* at Lake Tahoe, are given for two survey dates as well. Despite the high variability in TKN (standard error bars), differences due to date, site, and p/x were significant (ANOVA, $F = 8.749_{20,81}$, $p < .0001$). Data were \ln -transformed for statistical analyses, but are presented without transformation in this figure.

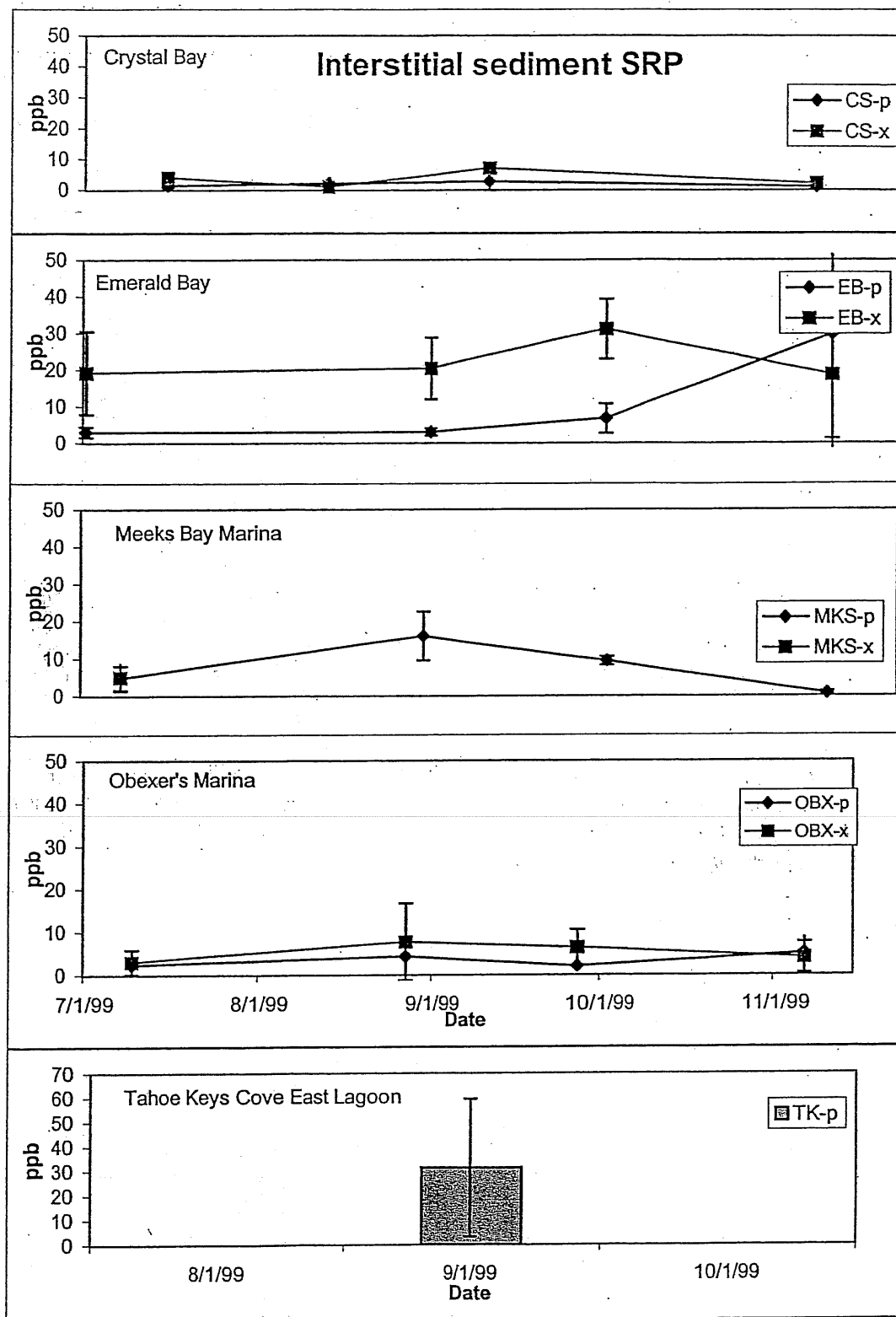


Figure 1.26a. Soluble reactive phosphorus (SRP) varied according to site, date, and the presence or absence of plants (p/x) at four Lake Tahoe sites in summer 1999 (ANOVA, $F = 7.387_{22,64}$, $<.0001$). In general, SRP was low and highly variable.

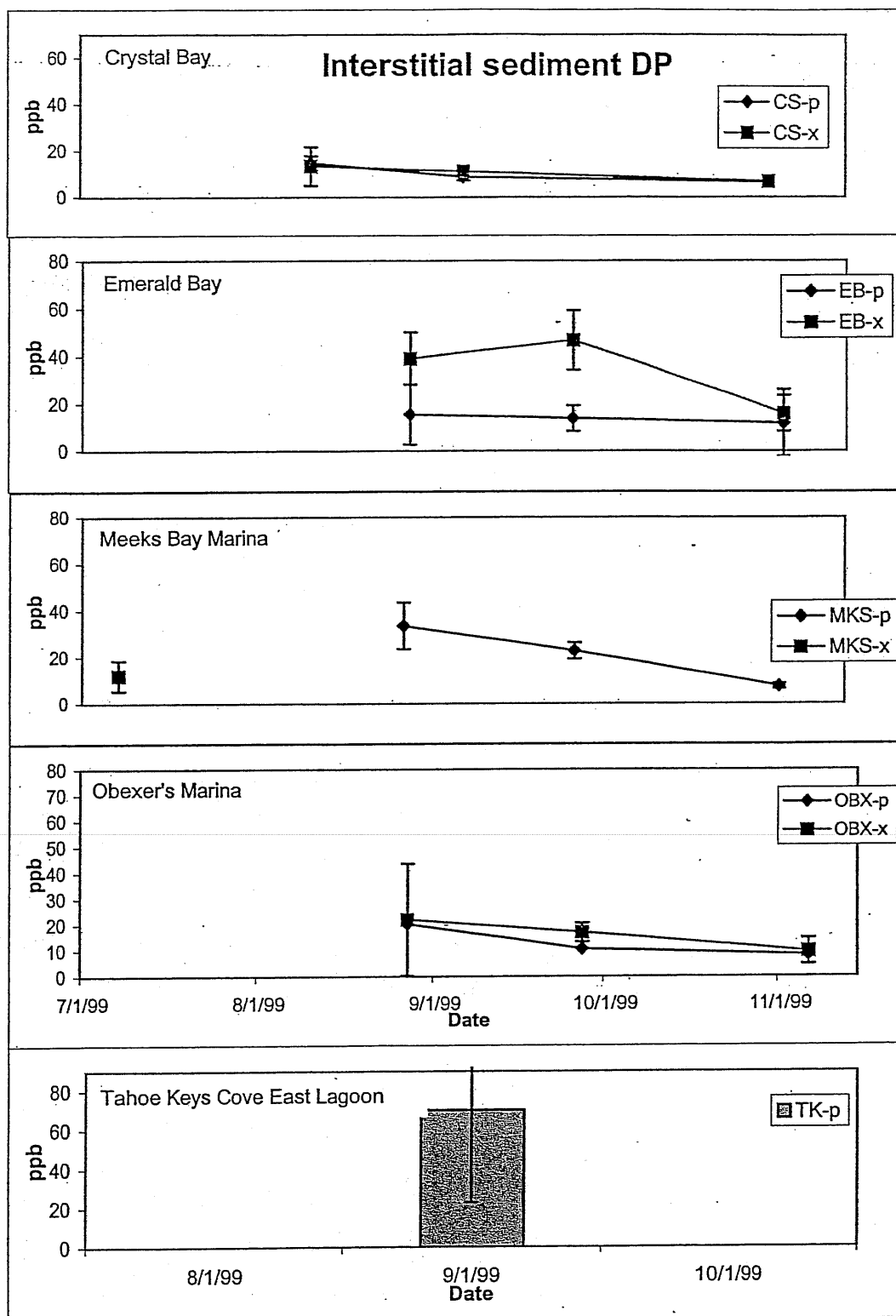


Figure 1.27. Dissolved phosphorus (DP) varied according to site, date, and the presence or absence of plants (p/x) at four Lake Tahoe sites (ANOVA, $F = 6.702_{9,56}$, $<.0001$). Dissolved phosphorus decreased in sediments over time from August 31, 1999 to November 5, 1999, but differences were not due to the presence or absence of plants.

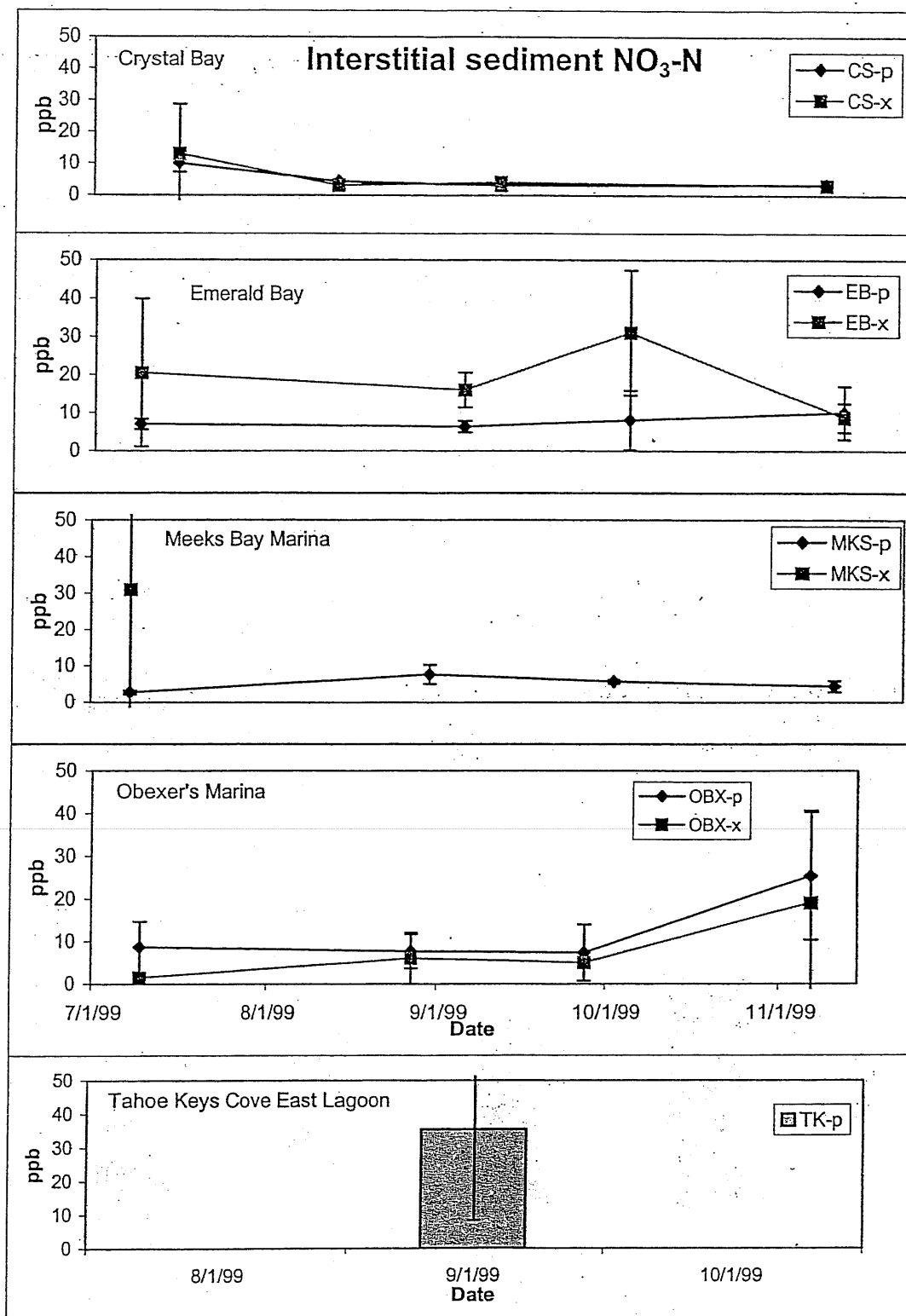


Figure 1.29. Concentrations of $\text{NO}_3\text{-N}$ varied according to site, date, and the presence or absence of plants (p/x) at four Lake Tahoe sites in summer 1999 (ANOVA, $F = 3.469_{9,64}$, $<.0001$). There were no consistent patterns of $\text{NO}_3\text{-N}$ in areas of plants and no plants, and among sites, $\text{NO}_3\text{-N}$ was lowest in sediment at Crystal Bay Marina.

Figure 1.30. Mean survivorship of *M. spicatum* plants grown for 9 weeks under treatment combinations of transplant site, source of *M. spicatum*, and source of sediment in transplant buckets. Reciprocal transplant sites and sources of sediment included the Tahoe Keys Cove East Lagoon (TK), Meeks Bay Marina (MKS), Boatworks Marina (BW), and Caspian Point (RKS). Sites that do not currently have *M. spicatum* populations BW and RKS. *Myriophyllum spicatum* plants used in this experiment were originally from either TK or MKS. *Myriophyllum spicatum* grew successfully at all of the transplant sites except where there was extreme wave action outside of BW.

Figure 1.31. Mean plant height of *M. spicatum* plants grown for 9 weeks under treatment combinations of transplant site, source of *M. spicatum*, and source of sediment in transplant buckets. Reciprocal transplant sites and sources of sediment included the Tahoe Keys Cove East Lagoon (TK), Meeks Bay Marina (MKS), Boatworks Marina (BW), and Caspian Point (RKS). Sites that do not currently have *M. spicatum* populations BW and RKS. *Myriophyllum spicatum* plants used in this experiment were originally from either TK or MKS. *Myriophyllum spicatum* grew successfully at all of the transplant sites except where there was extreme wave action outside of BW. It should be noted that not all treatments had same number of reps for height response variable. Plant heights were averaged among the plants that survived in transplant buckets. Zero's associated with non-survivors have been omitted from this analysis.

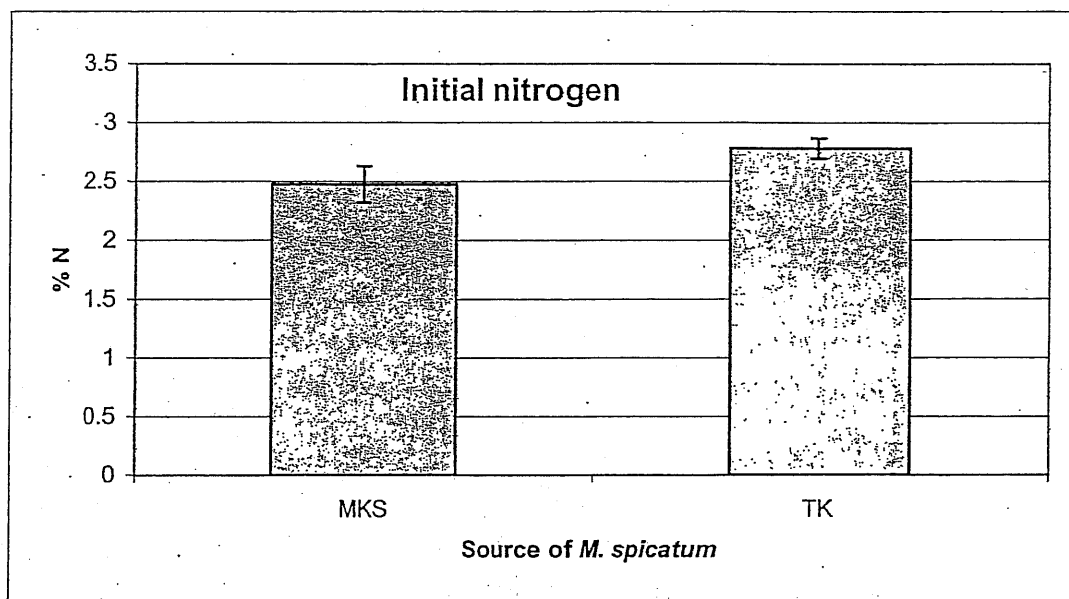


Figure 1.32a. Initial nitrogen concentrations were higher in *M. spicatum* from the Tahoe Keys (TK) than in plants from Meeks Bay (MKS) (ANOVA, $F = 9.162_{1,4}$, $p = .0389$).

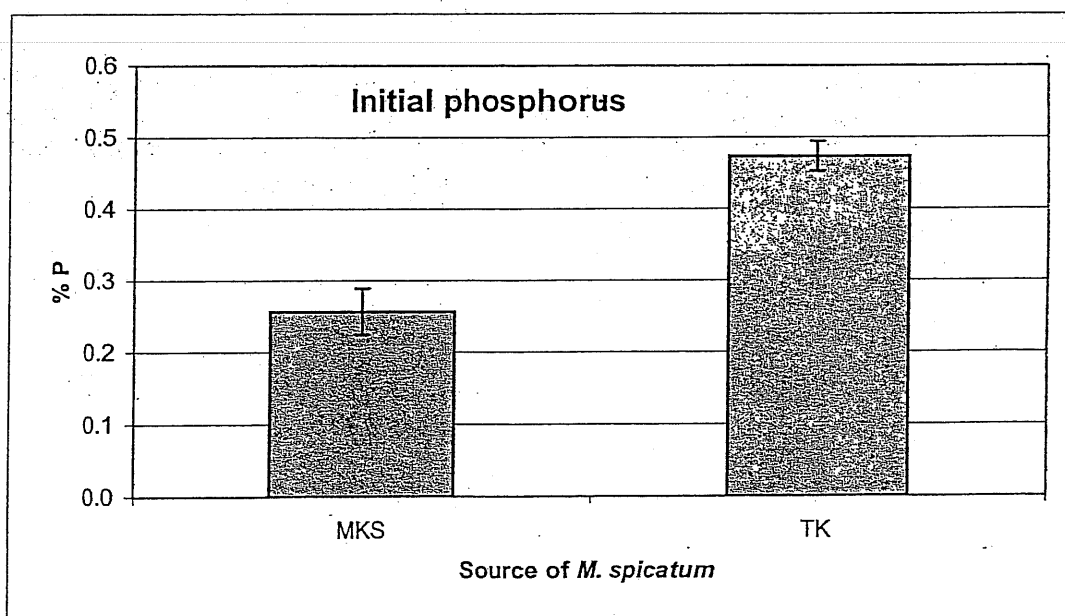


Figure 1.32b. Initial phosphorus concentrations were higher in *M. spicatum* from the Tahoe Keys (TK) than in plants from Meeks Bay (MKS) (ANOVA, $F = 96.022_{1,4}$, $p = .0006$).

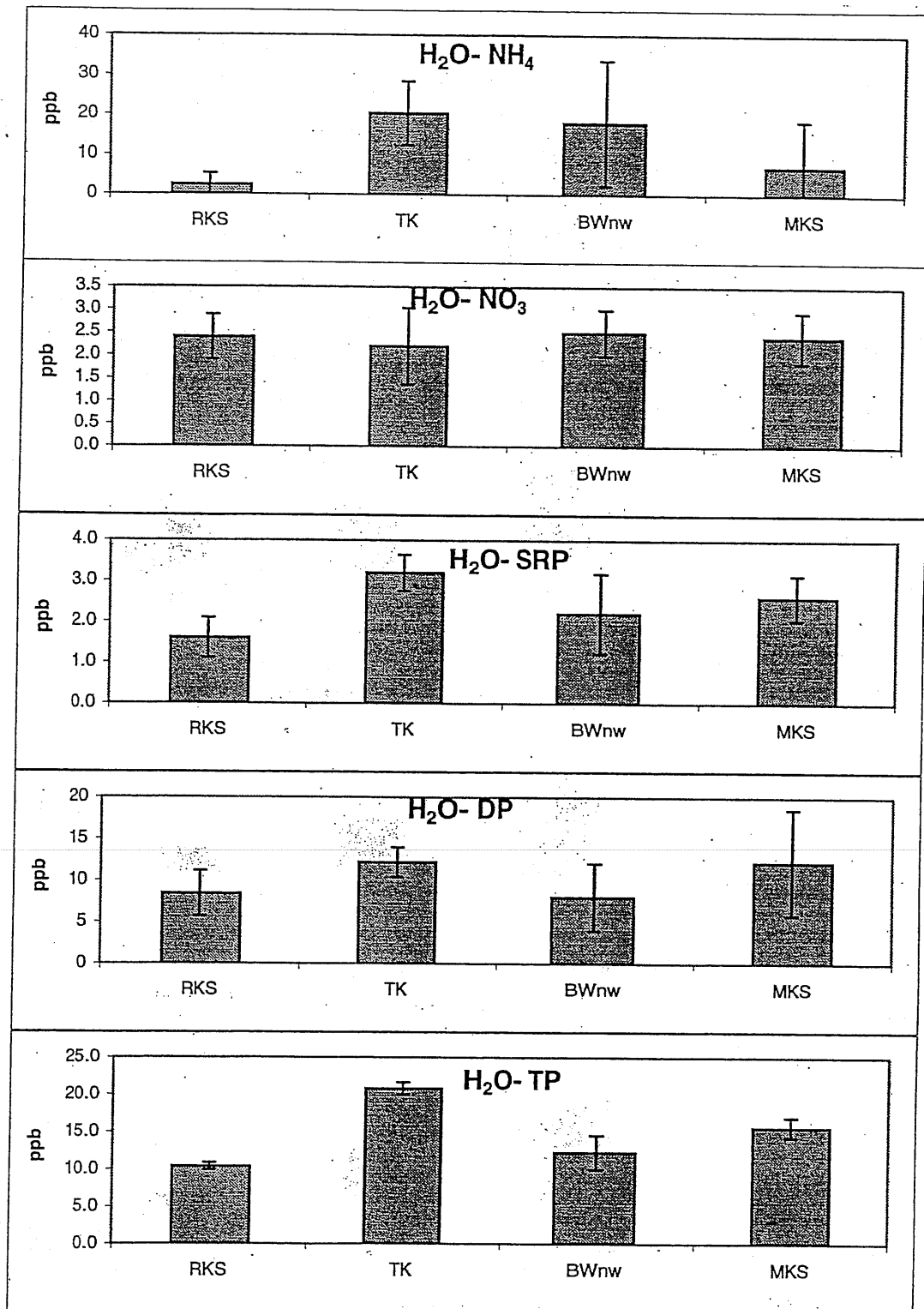


Figure 1.33a. Nutrients ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, SRP, DP, and TP) in lake water collected on August 21, 1999 from transplant sites: Kaspian Point (RKS), Tahoe Keys Cove East Lagoon (TK), Boatworks Marina (BWnw), and Meeks Bay (MKS). Nutrients concentrations are highly variable (standard error bars), but appear to be highest at the Tahoe Keys for all nutrients except $\text{NO}_3\text{-N}$.

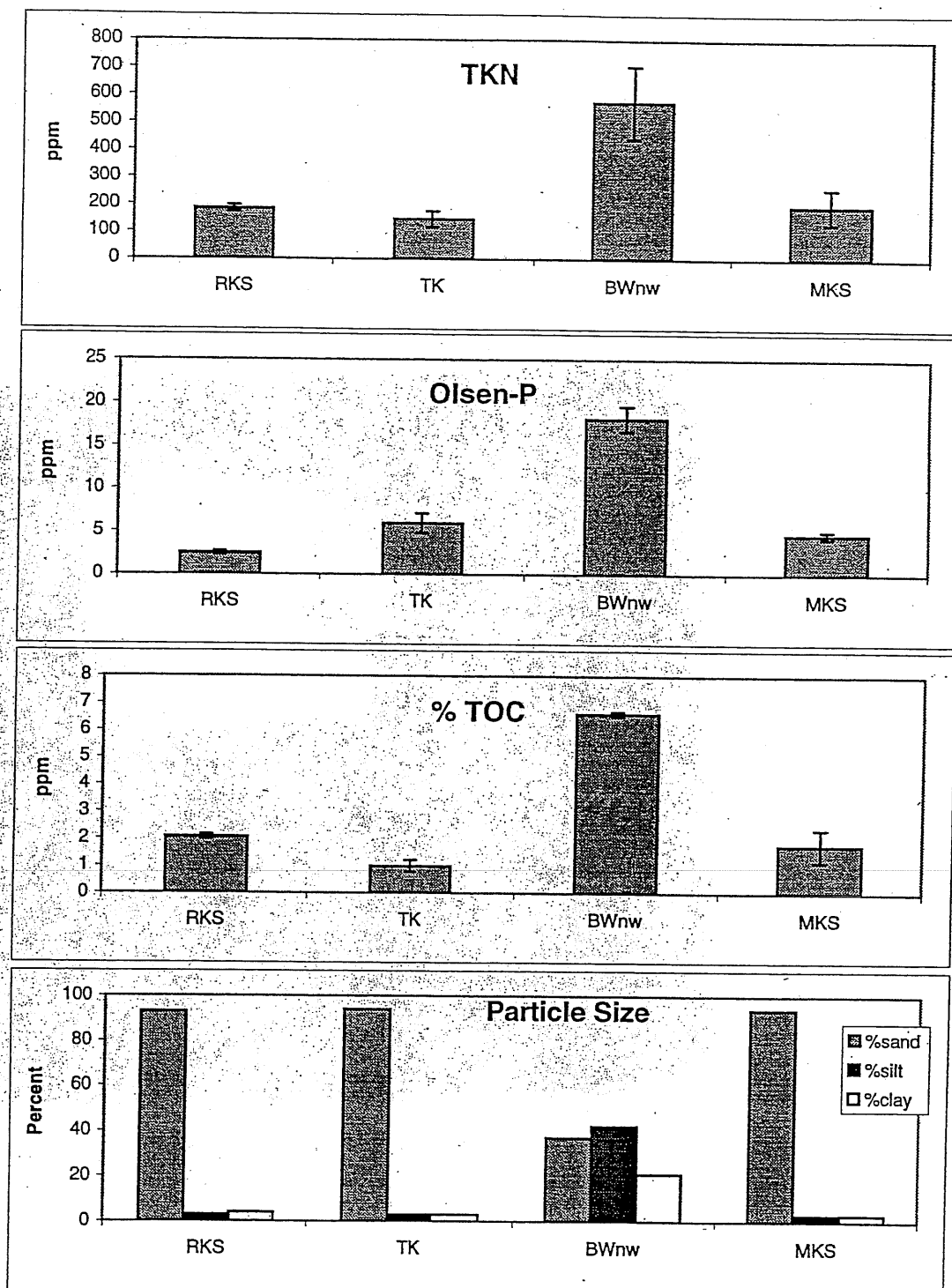


Figure 1.33c. Nutrients (TKN and Olsen-P), organic matter (TOC), and particle size distributions of transplant sediments collected and dried on August 21, 1999 from transplant sites: Kaspian Point (RKS); Tahoe Keys Cove East Lagoon (TK), Boatworks Marina (BWnw), and Meeks Bay (MKS). Sediment from Boatworks Marina appears to have been the most different. It had the highest TKN, Olsen-P and TOC, and the widest distribution of sand, silt and clay. Other sites had lower nutrient contents and were composed primarily of sand.



Figure 2.2. Outdoor sediment-plant microcosms to assess nutrient release from senescing macrophytes, *Myriophyllum spicatum* and *Elodea canadensis*, as well as phytoplankton chlorophyll-*a* response.

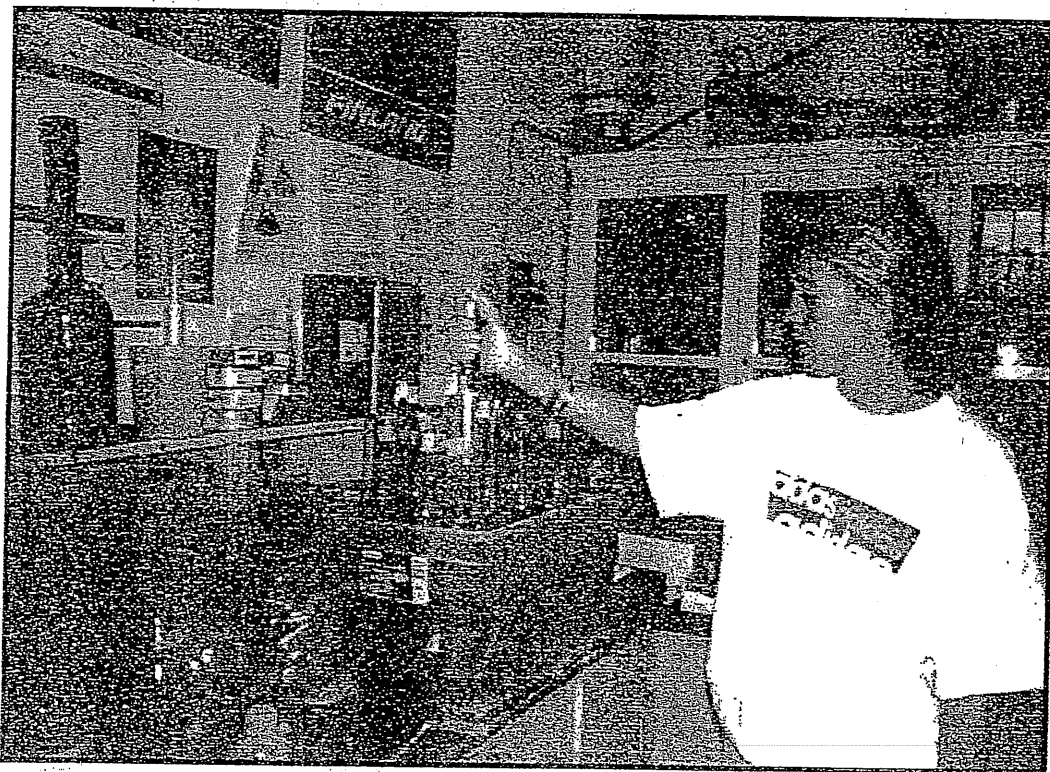


Figure 2.4. Daily sampling 1-ml aliquots from stirred water columns of ^{32}P in hydroponic aquatic plant microcosms for liquid scintillation counting.

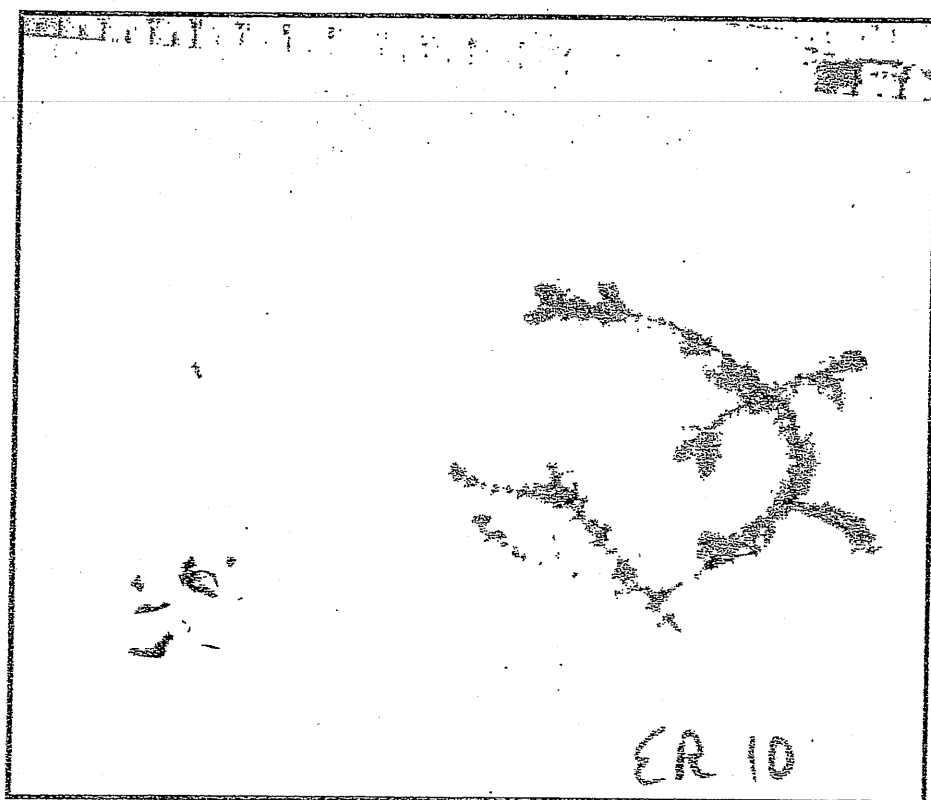
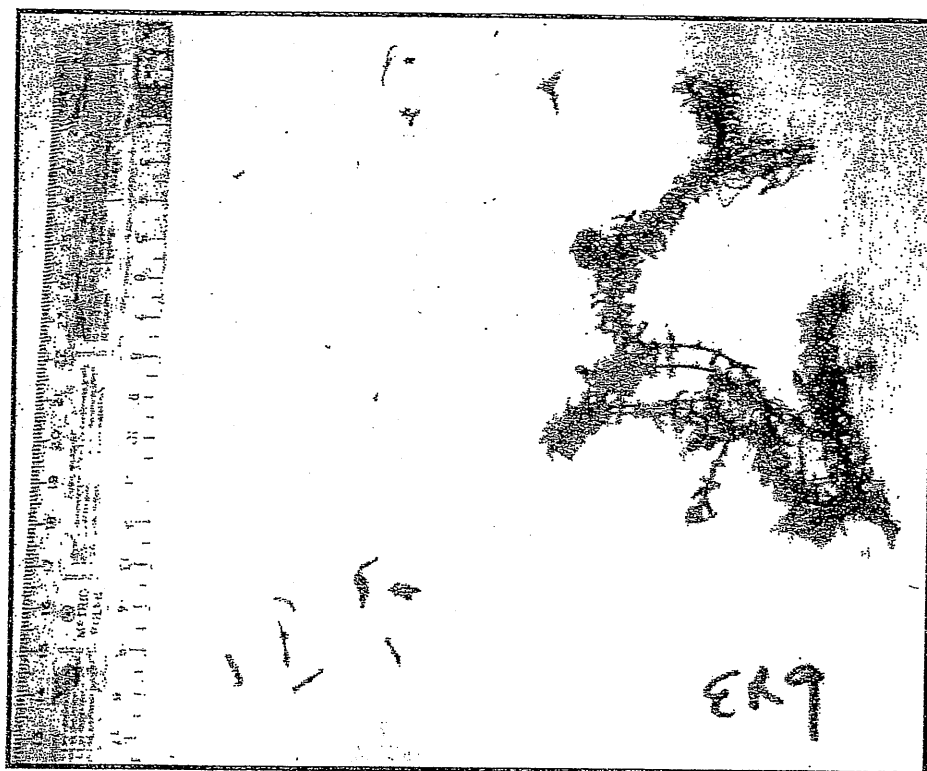


Figure 2.5b. Partially senescent *Elodea canadensis* at the end of the ^{32}P hydroponic aquatic plant microcosm experiment.

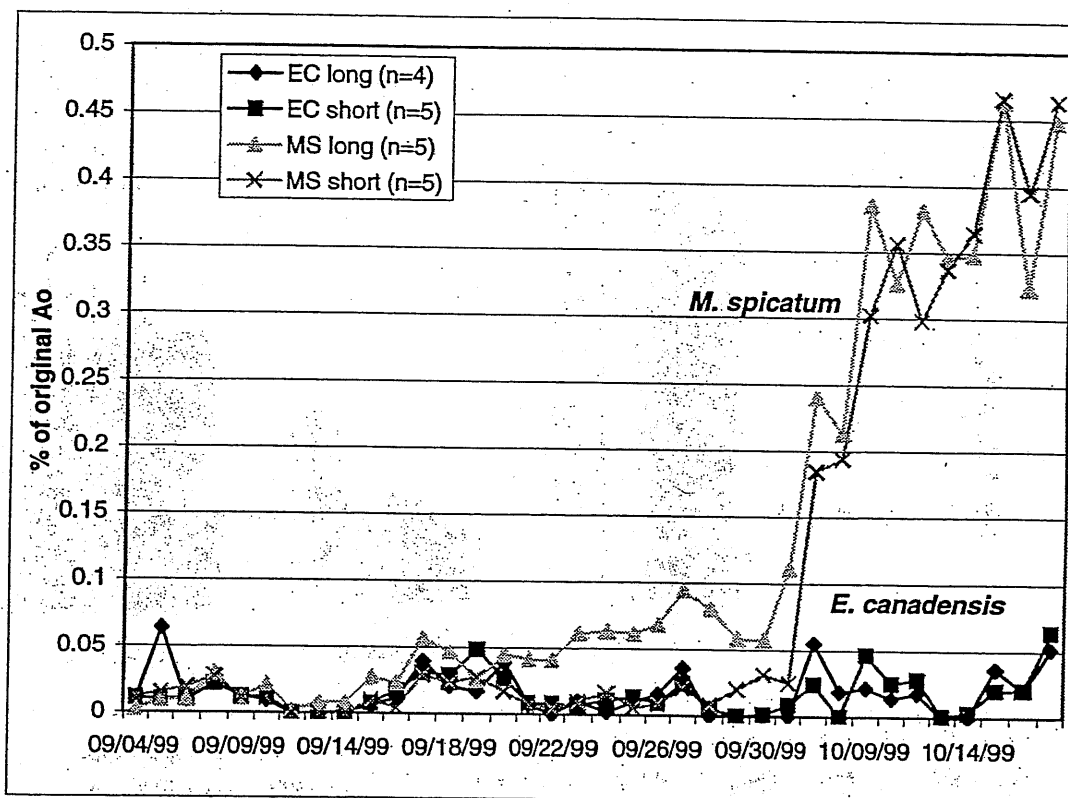


Figure 2.7. ^{32}P detected in water columns of *M. spicatum* (MS) and *E. canadensis* (EC) under long and short-day photoperiods as a percent of the original amount present in sealed root compartments. The pattern of results is the same as in Figure 2.6. ^{32}P activities are higher in MS microcosms over the 45-day experimental period than in EC microcosms.

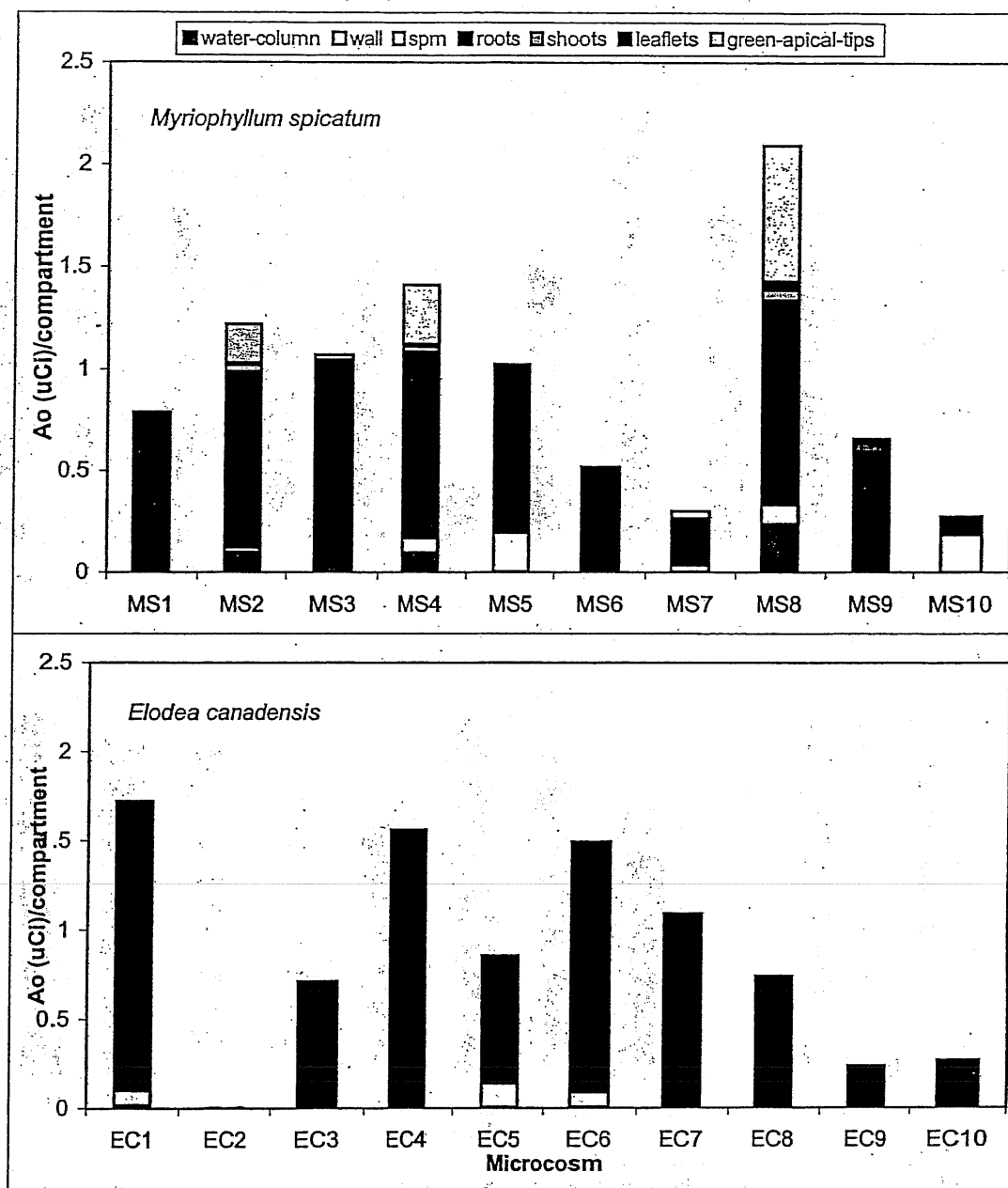


Figure 2.9. ^{32}P activity in biological components of *M. spicatum* (MS) and *E. canadensis* (EC) microcosms at the end of the experiment. Microcosms 1-5 represent long-day treatments for both plant species and microcosms 6-10 had short-day treatments. Suspended particulate matter (SPM) in 20-ml of water from microcosms was collected on filters prior to acid digestion. Biofilm (wall) on side walls of the microcosms were also included in this analysis. Plant parts of MS and EC included roots, shoots, leaflets that had fallen off shoots prior to the final day, and green-apical meristems (3-4cm). Microcosm EC2 has been excluded because it received a double dose of ^{32}P activity at the beginning of the experiment. Among biological components, most of the ^{32}P was detected in plant roots.

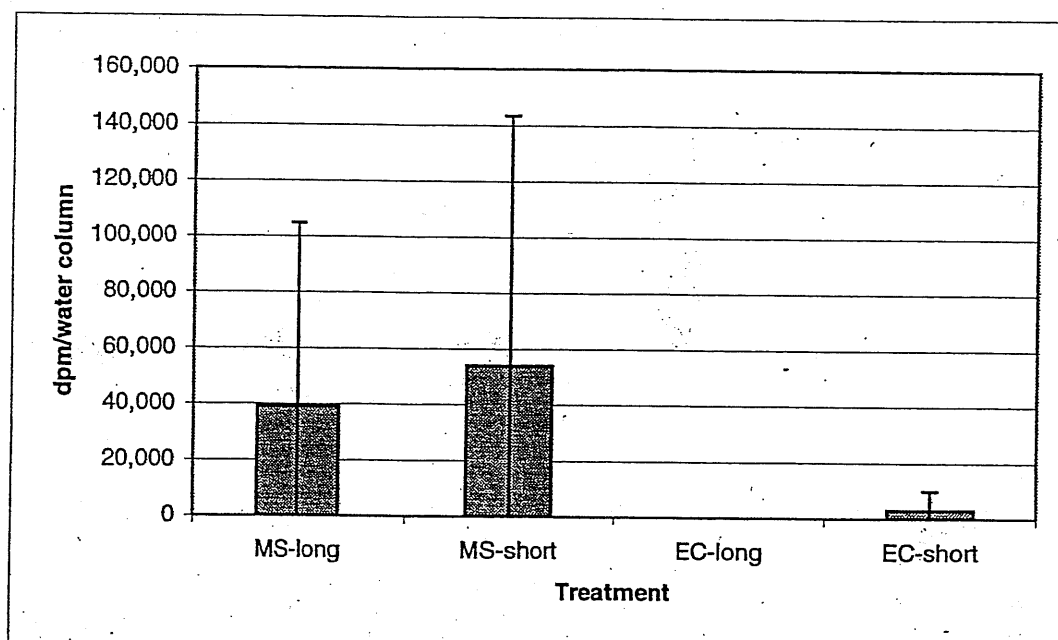


Figure 2.11. Mean ^{32}P activity of suspended particulate matter (SPM) in water columns of *M. spicatum* (MS) and *E. canadensis* (EC) under long and short-day photoperiods. Large error bars (standard deviations) represent high variability within treatments. A one-way ANOVA with marginal significance confirms that specific activities in SPM of MS microcosms were greater than those in EC microcosms ($F = 3.641_{1,18}$, $p = .0725$). Specific activities of SPM were not different due to photoperiod in this experiment.

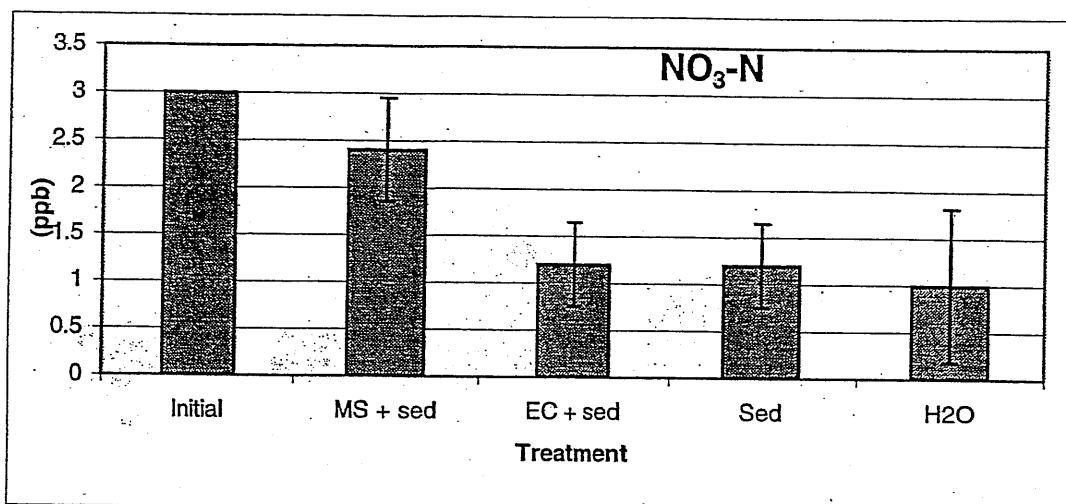


Figure 2.14. Mean NO₃-N concentrations in water columns of in plant-sediment microcosms. On average, NO₃-N concentrations were greater in microcosms containing *M. spicatum* (MS) and in the initial unfiltered water from Sunnyside than in microcosms with *E. canadensis* (EC) and controls of sediment (Sed) and lake water (H2O) (Kruskal-Wallis, $\chi^2 = 13.231_4$, $p < .0102$).

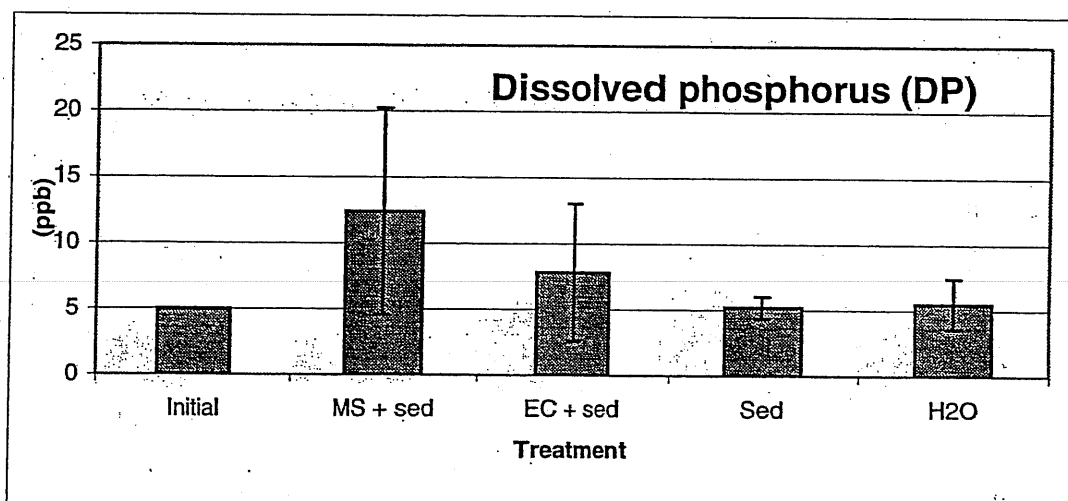


Figure 2.15. Mean DP concentrations in water columns of plant-sediment microcosms. Dissolved phosphorus (DP) concentrations appear to be greater in microcosms containing *M. spicatum* (MS) than *E. canadensis* (EC) and controls of sediment (Sed) and lake water (H2O), but differences were not significant.

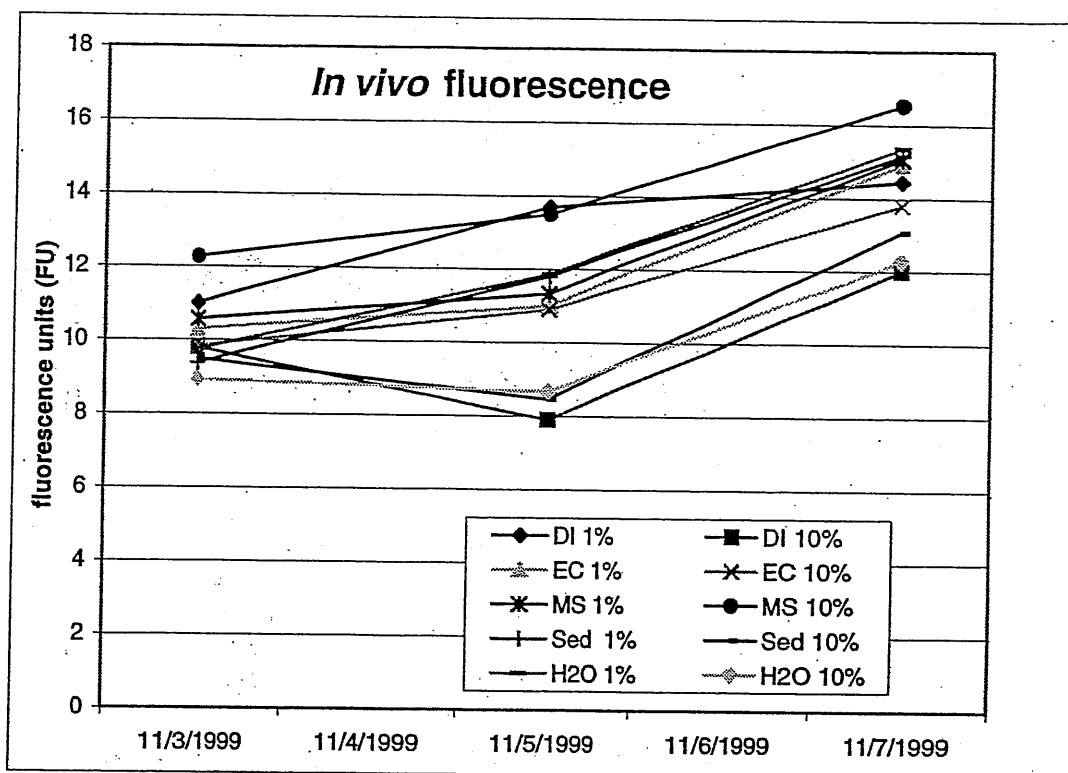


Figure 2.18. Changes in *in vivo* fluorescence of natural phytoplankton populations in bioassay flasks over six days. Treatments refer to 1% and 10% concentrations of exudates filtered from microcosms containing *M. spicatum* (MS), *E. canadensis* (EC), sediment without plants, and lake water without sediments and plants. A third control in the bioassay was deionized water at 1% and 10% concentrations in bioassay flasks. *In vivo* fluorescence increased over the six day period in all flasks, but to the greatest extent in treatments of *M. spicatum*.

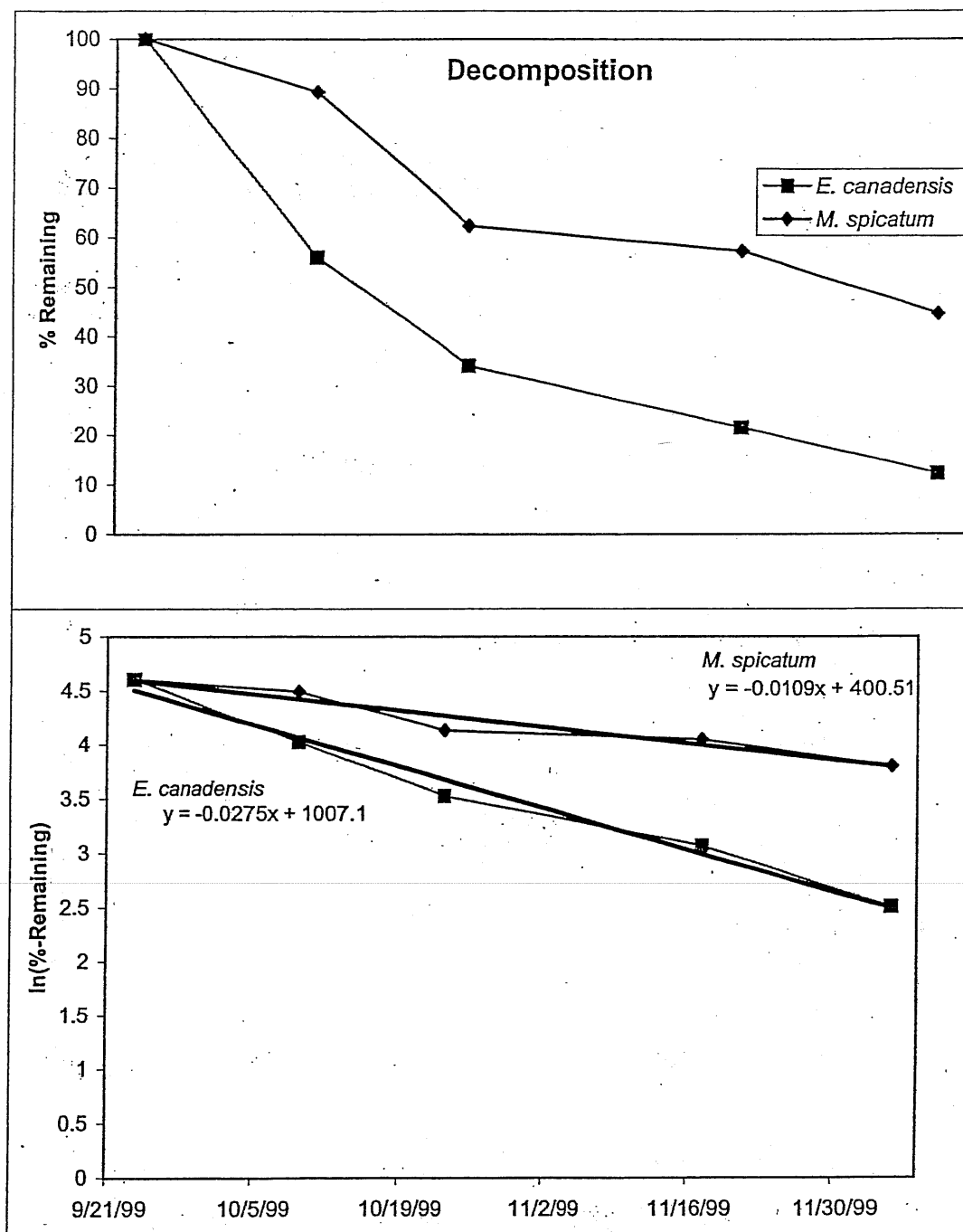


Figure 2.20. Decomposition of *M. spicatum* and *E. canadensis* at the Tahoe Keys Cove East Lagoon in Fall, 1999. Percent remaining is based on the dry weight (g) of plant remains in mesh bags after a period of decomposition, calculated from an initial wet weight:dry weight ratio. Error bars are small, and represent standard deviations. The linear fits on the $\ln(\% \text{-remaining})$ figure revealed that the decay constants for *E. canadensis* ($r = -0.0275$) was greater than that for *M. spicatum* ($r = -0.109$), and that that decomposition of *E. canadensis* ($R^2 = 0.98$) followed an exponential decay pattern better than *M. spicatum*

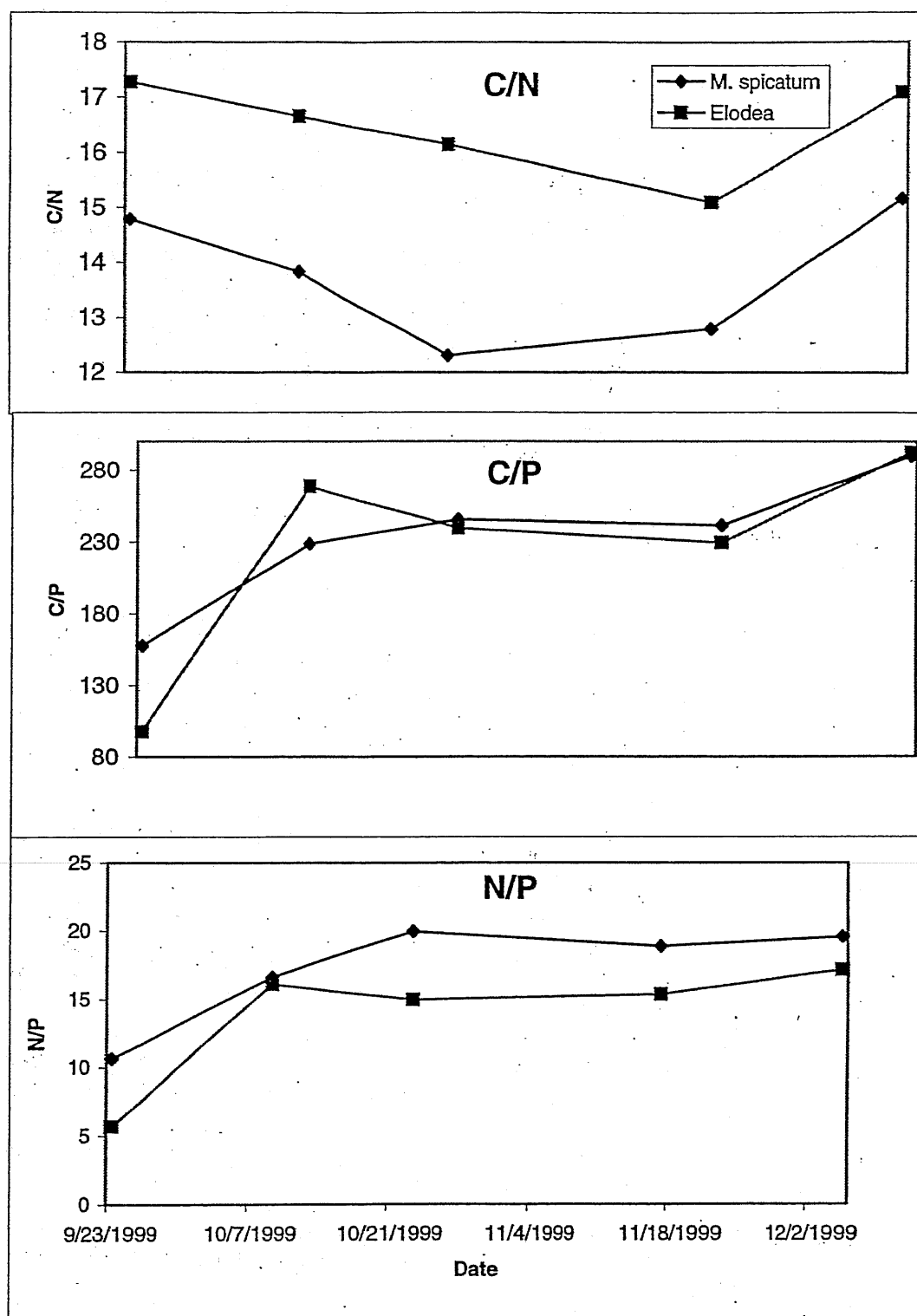


Figure 2.22. Nutrient ratios in contents of *M. spicatum* and *E. canadensis* mesh bags after decomposition. All mesh bags were placed in the Tahoe Keys Cove East Lagoon on September 23, 1999, and dates in this figure indicate when bags were harvested from decomposition. Error bars represent standard deviations.

Table 1.2. Mean height of *M. spicatum* changed according a three-factor ANOVA with interaction and nesting of site, date and the repeated measurement of points along survey transects at four Lake Tahoe locations in Summer 1999. We found significant effects of these factors on plant height (ANOVA, $F=11.277_{51,277}$, $p<.0001$)

Source	DF	F Ratio	p
Date	3	9.1	<0.0001
Site	3	61.88	<0.0001
Date*Site	9	10.84	<0.0001
Point(Site)	36	7.35	<0.0001

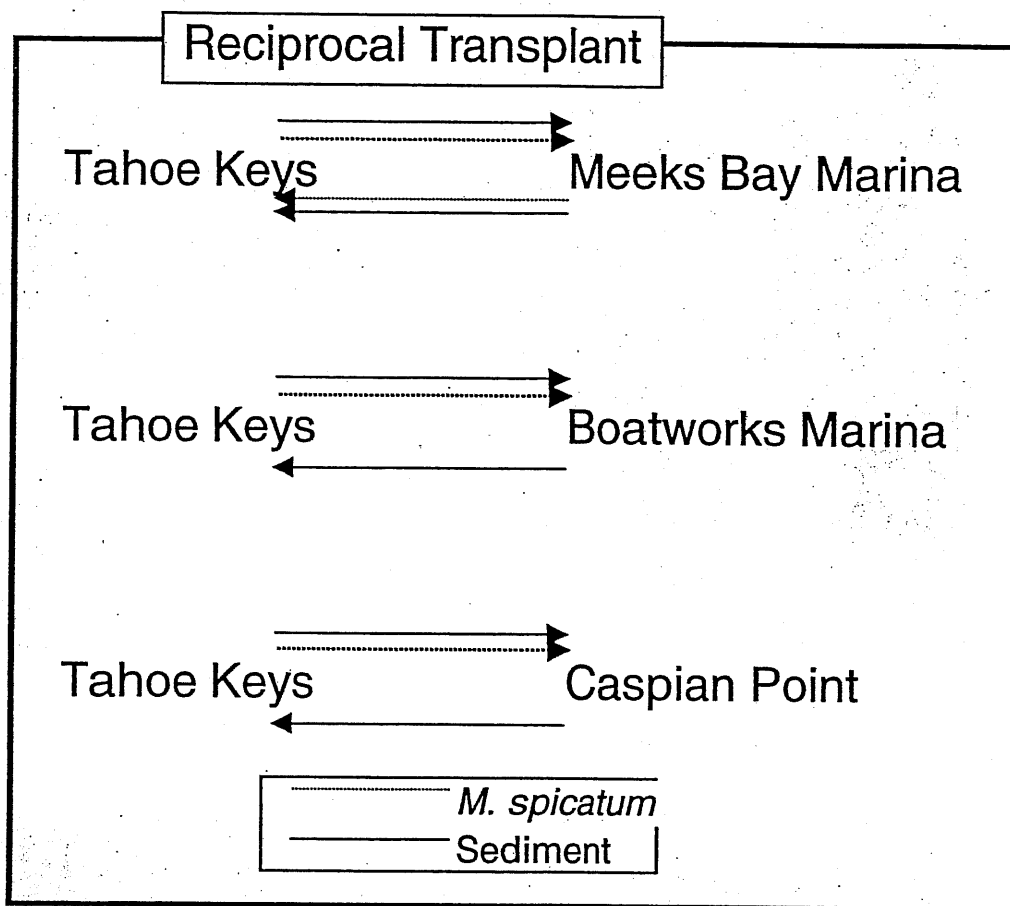


Figure 1.11. Experimental scheme for reciprocal transplant. *Myriophyllum spicatum* from the Tahoe Keys and Meeks Bay Marina were grown under various combinations of site and sediment source in plastic containers for nine weeks.

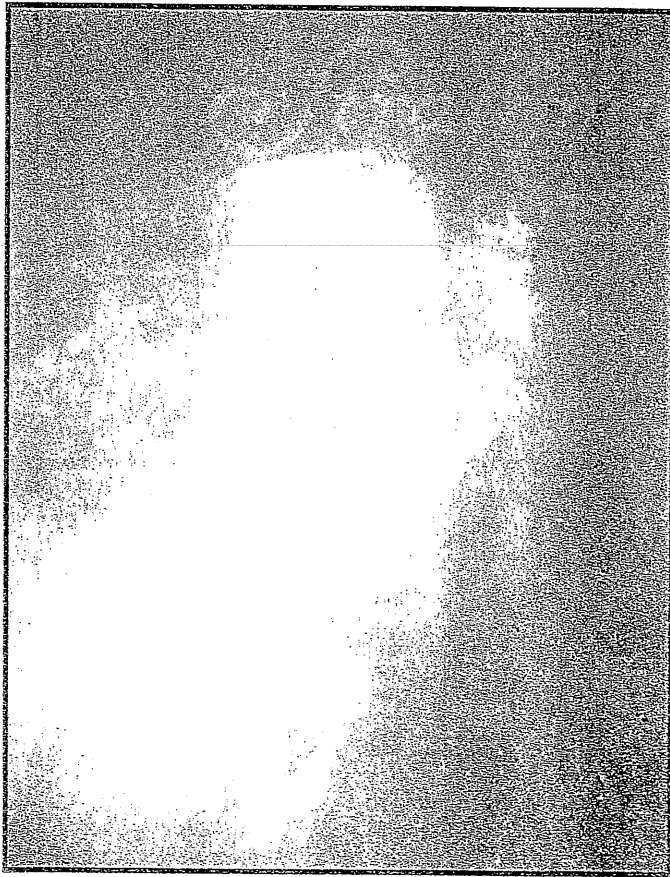


Figure 1.12. Top: sampling interstitial sediment pore water from transplant containers with *Myriophyllum spicatum* on the final day of the experiment. Bottom: *In situ* growth of *Myriophyllum spicatum* in plastic buckets under reciprocal transplant treatments of sediment source and transplant site.

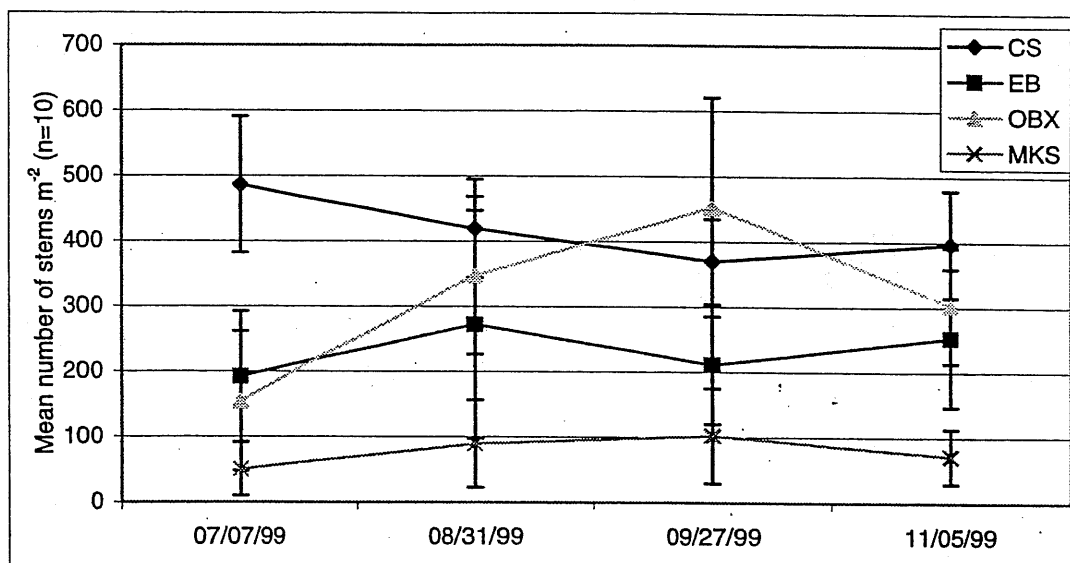


Figure 1.14 . Changes in mean density of *M. spicatum* at four Lake Tahoe locations over Summer 1999: Crystal Bay Marina (CS), Emerald Bay (EB), Obexer's Marina (OBX), and Meeks Bay Marina (MKS). Differences by site, date, and sampling point along transects were significant ($F = 27.964_{53,104}$, $p < .0001$). Data were transformed in statistical analysis to meet ANOVA assumptions of normality, but are presented in raw form here.

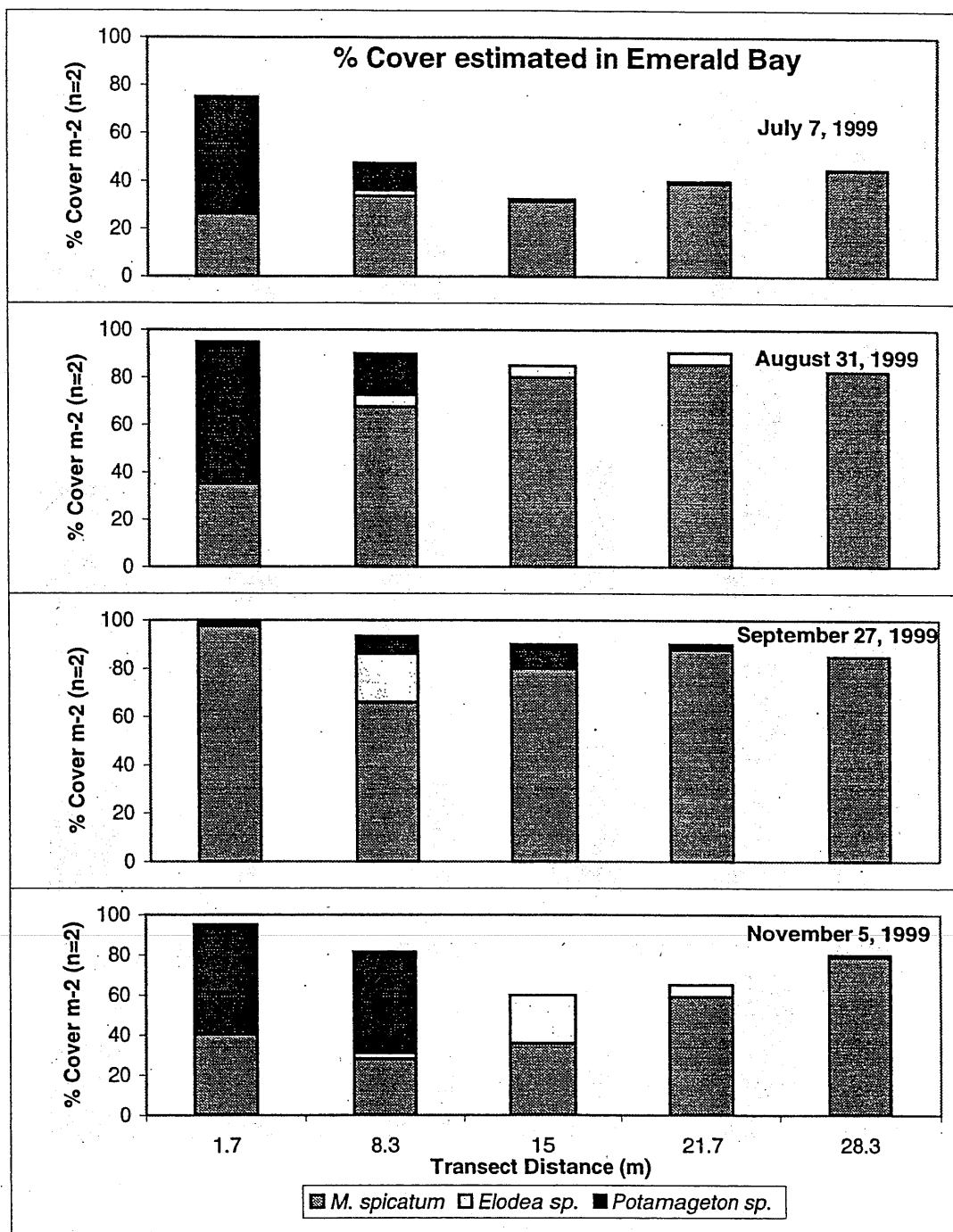


Figure 1.16a. The estimated percent cover of *M. spicatum* at Emerald Bay increased from July 7, 1999 to September 27, 1999, displacing other native macrophytes. By November 5, 1999 the percent cover of *M. spicatum* decreased and that of native plants increased.

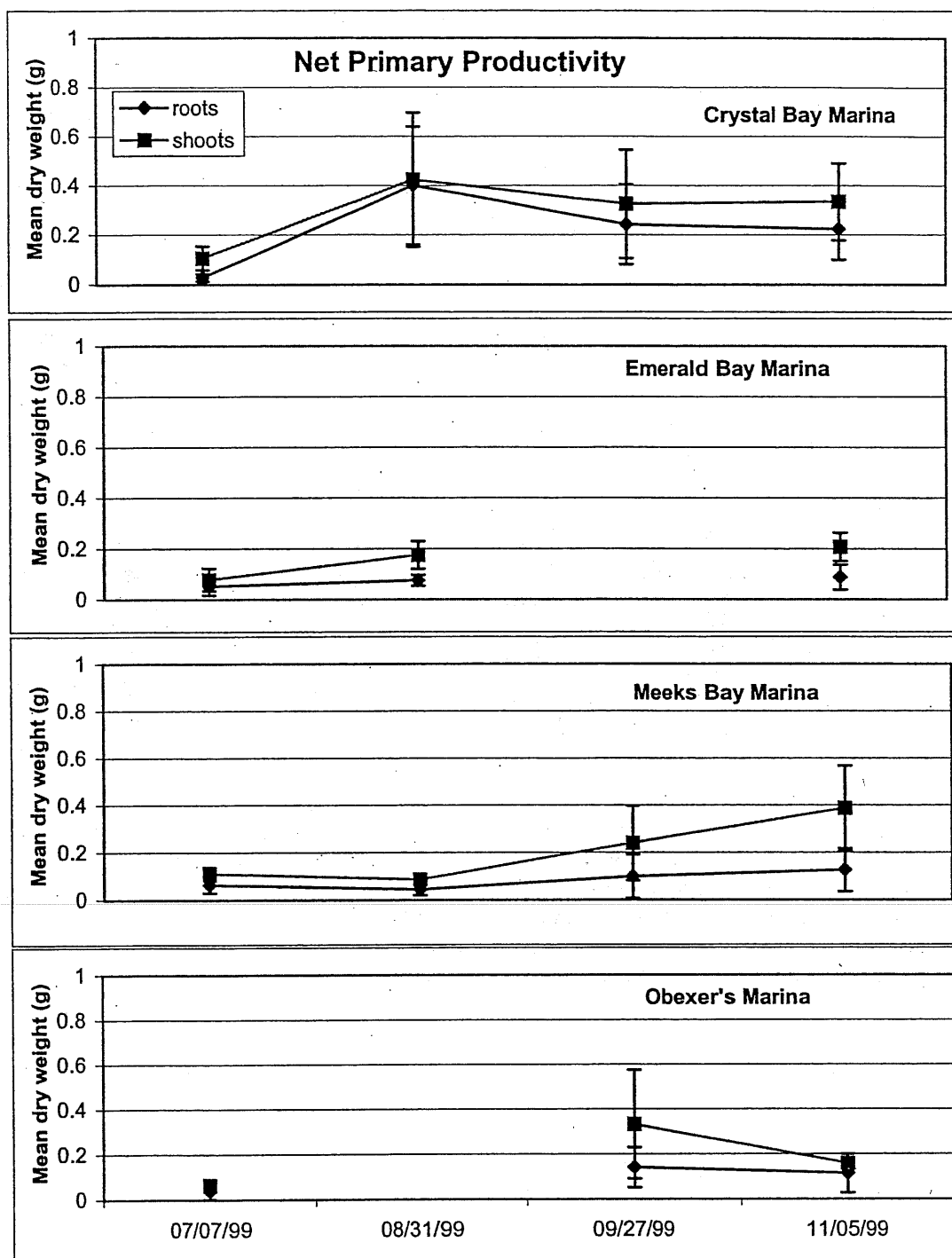


Figure 1.17a. Net primary productivity (NPP- mean biomass) of *M. spicatum* increased from July 7, 1999 through September 27, 1999. It decreased slightly by November 5, 1999. Plant biomass was greater, on average, at Crystal Bay marina than at the other sites. Differences biomass of roots and shoots were significant according to survey site and date (ANOVA, $F = 13.048_{14,121}$, $p < .0001$). On the August sampling date, Meeks Bay had six sampling points ($n=6$), and on the September date it had only three ($n=3$).

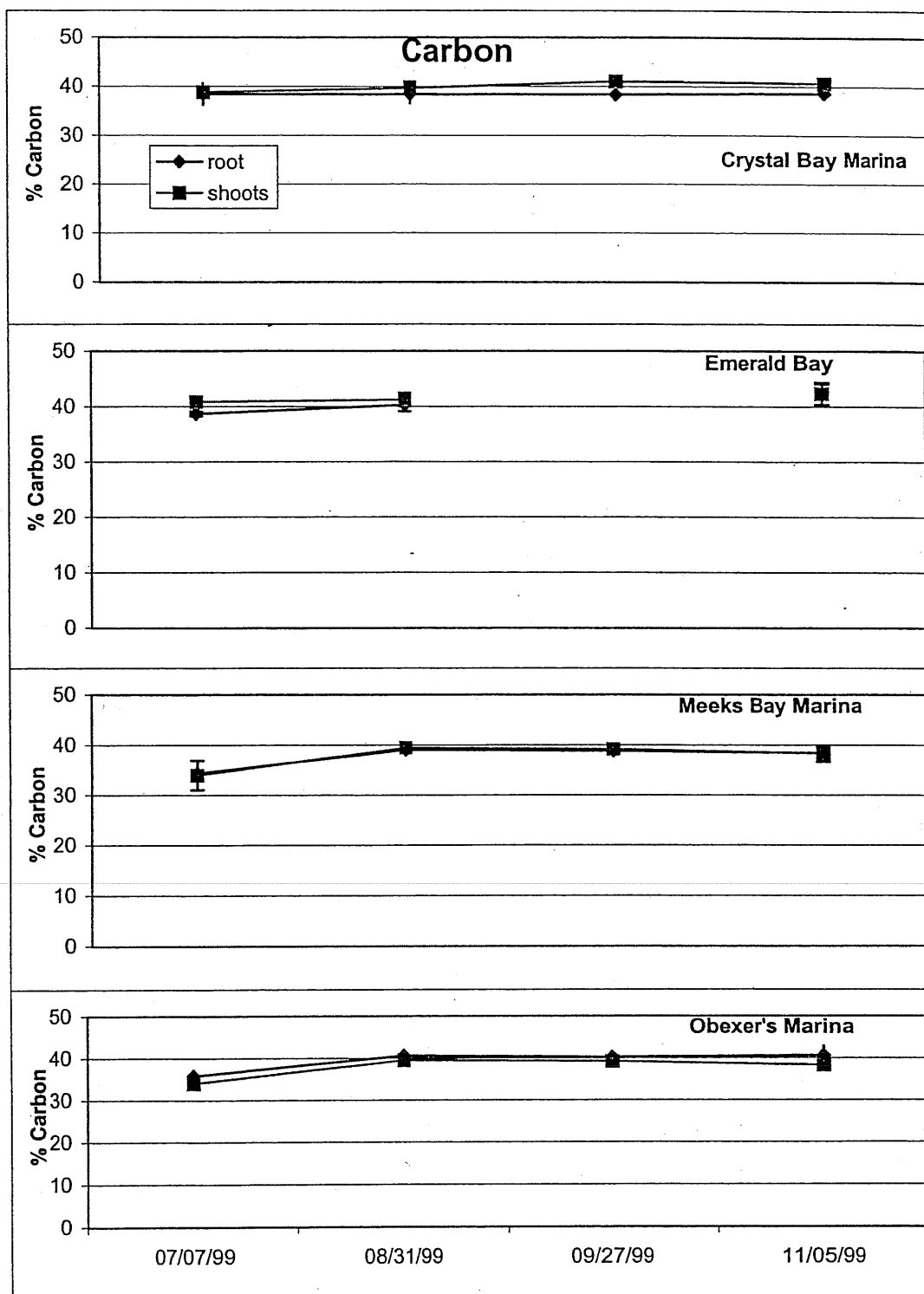


Figure 1.18a. Total %-C of *M. spicatum* plants varied according to the Site*Date interaction and root and shoot plant parts, and the 3-way interaction of Site*Date*root/shoot ($F = 11.443_{29,112}$, $p < .0001$). Carbon seems to increase slightly over the summer at all four sites. Shoot carbon is slightly higher than root carbon except at Obexer's Marina. Missing points are the result of inadequate plant biomass for nutrient analyses.

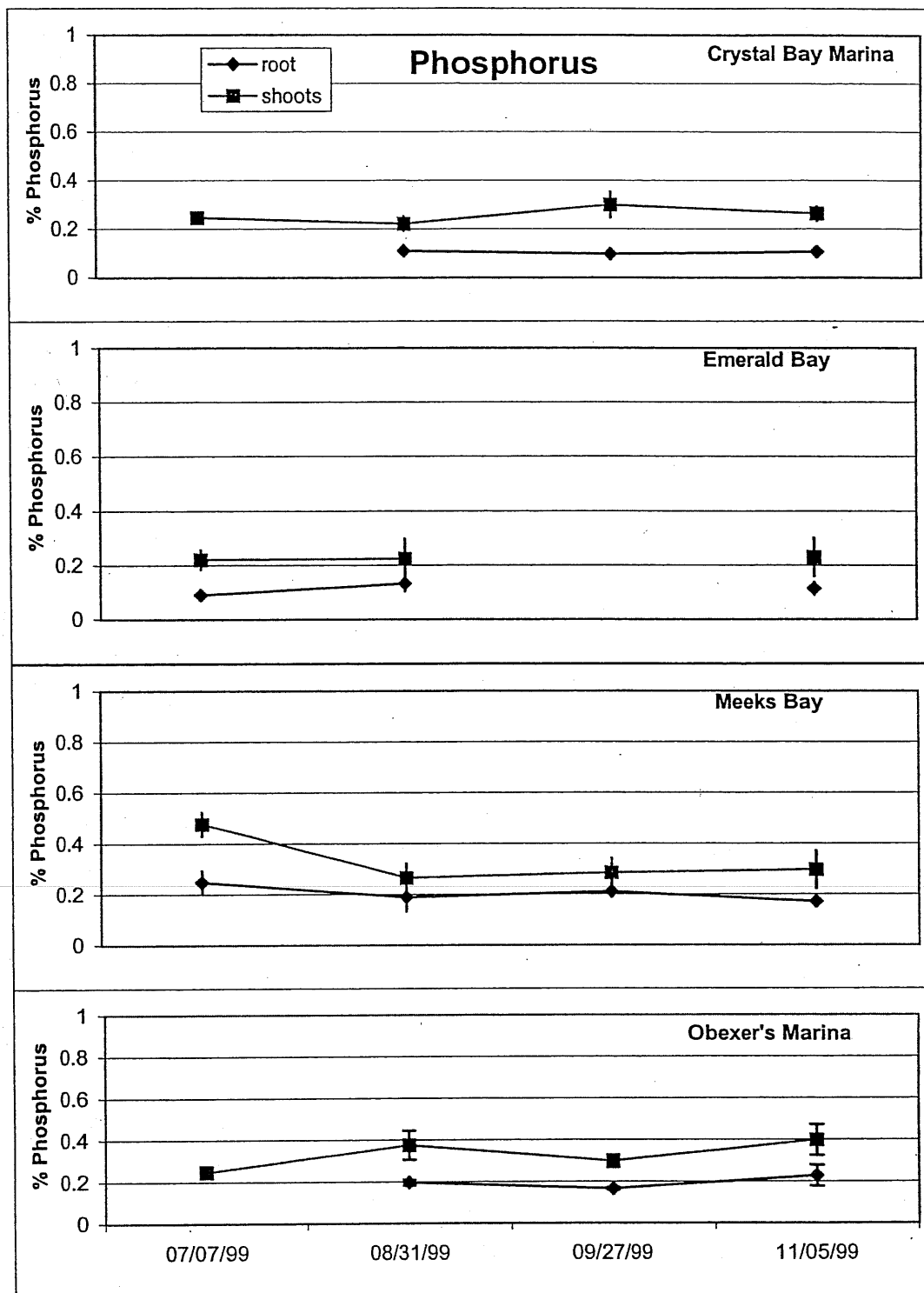


Figure 1.18c. Total %-P of *M. spicatum* plants varied according to the site*date interaction and root and shoot plant parts ($F = 3.483_{15,110}$, $p < .0001$). For P, roots are always higher than shoots. There is no obvious trend in % P data any of the sites over the summer, except, at Meeks Bay where P appears to have decreased with time. Missing points are the result of inadequate plant biomass for nutrient analyses.

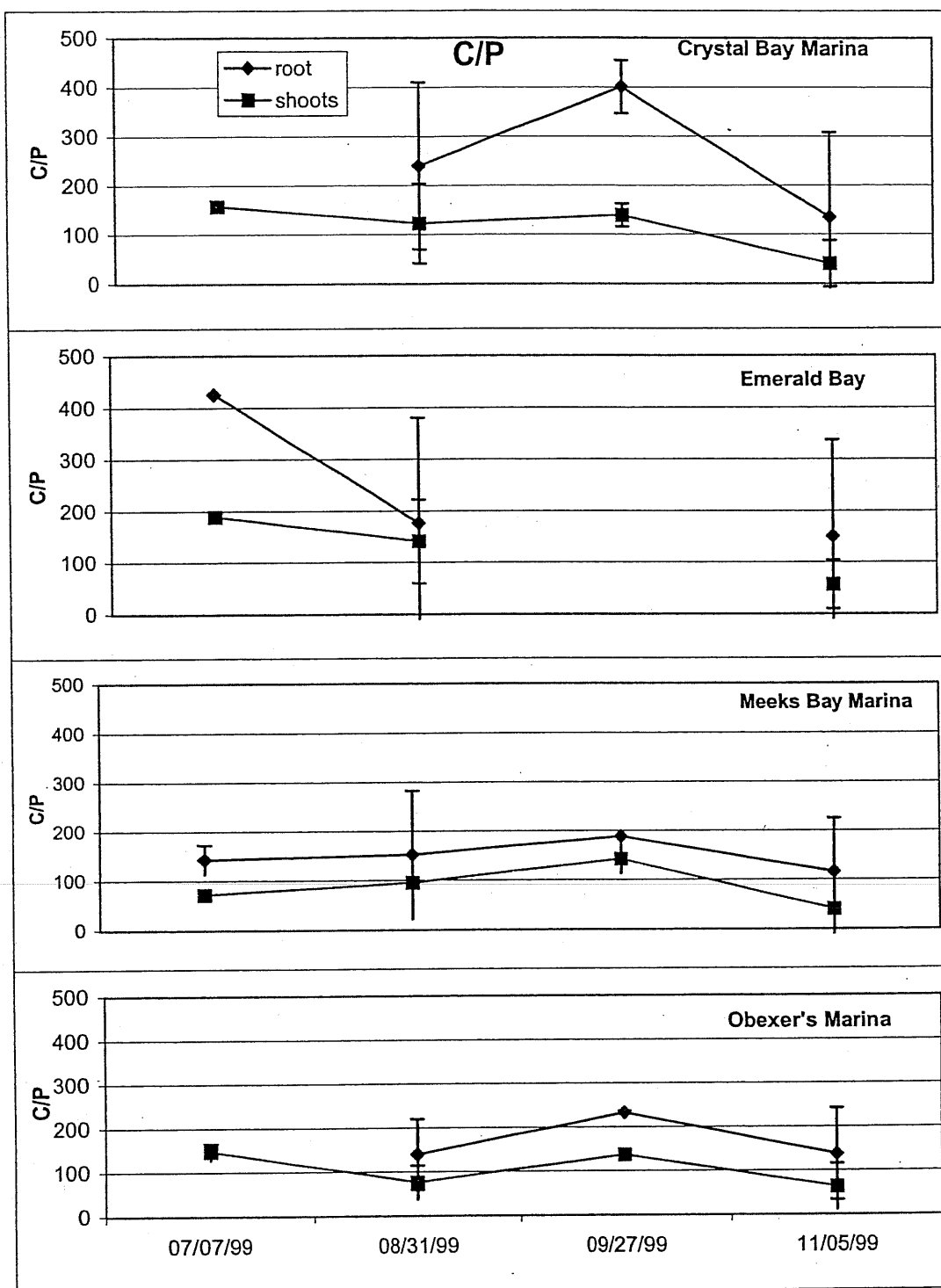


Figure 1.19b. Ratios of C/P in *M. spicatum* plants varied by Site*Date concatenations and root vs. shoot plant parts (ANOVA, $F = 3.48_{15,110}$, $p < .0001$). C/P appears to increase until September 27, 1999, and then by November 5, 1999, the C/P ratio has fallen substantially. This means that by the end of the summer roots and shoots have become more P rich. In all cases, shoots have a lower C/P ratio, suggesting that they are more P rich than roots. Missing points are the result of inadequate plant biomass for nutrient analyses.

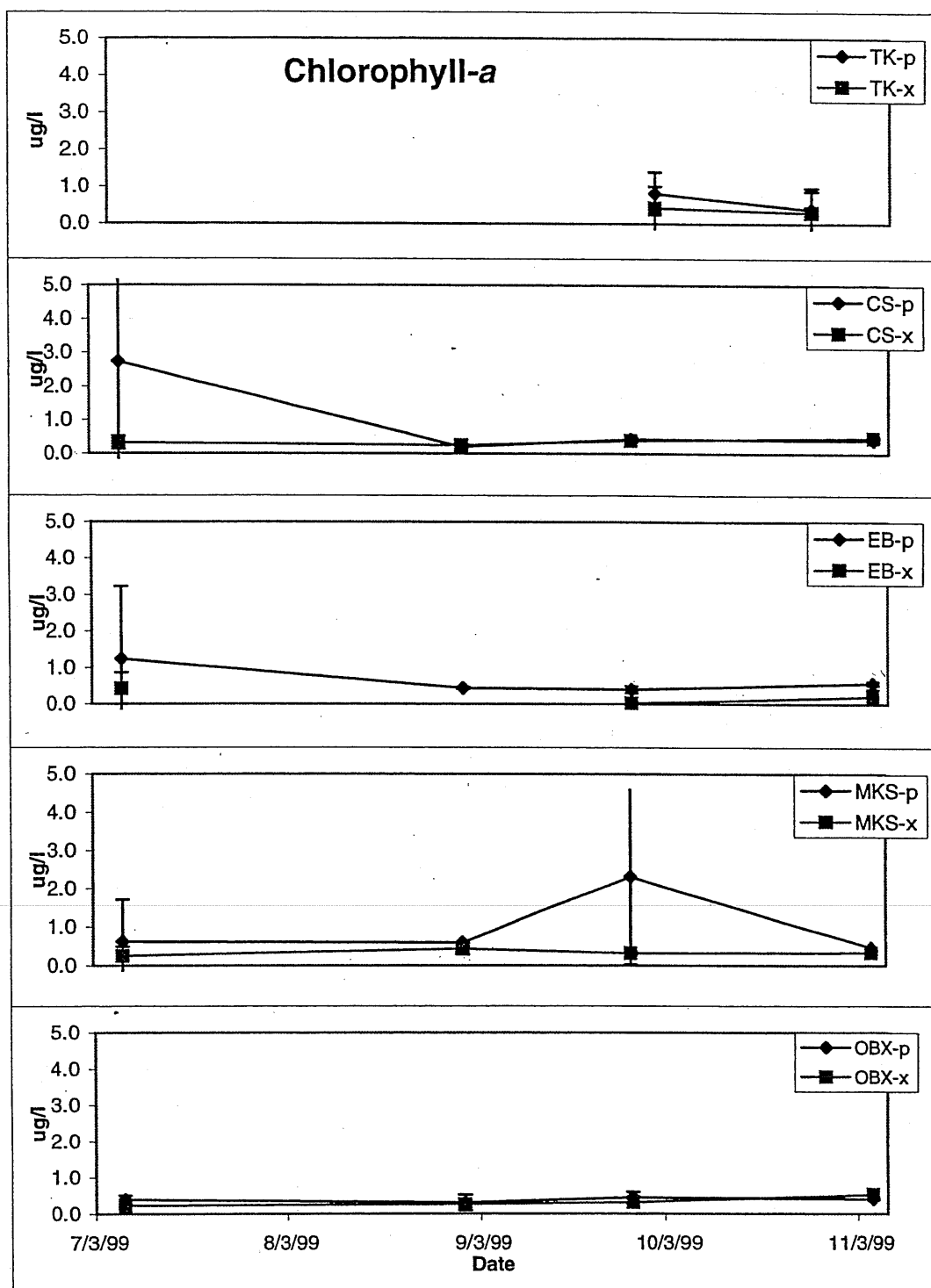


Figure 1.20. Mean chlorophyll-a in lake water on four dates in Summer 1999 in areas with (p) and without plants (x) from the Tahoe Keys (TK) and four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). The ranking of chlorophyll-a in an extension of Kruskal-Wallis differed according to survey date, site, and the presence or absence of *M. spicatum* plants at sites ($F = 8.972_{23,136}$, $p < .0001$).

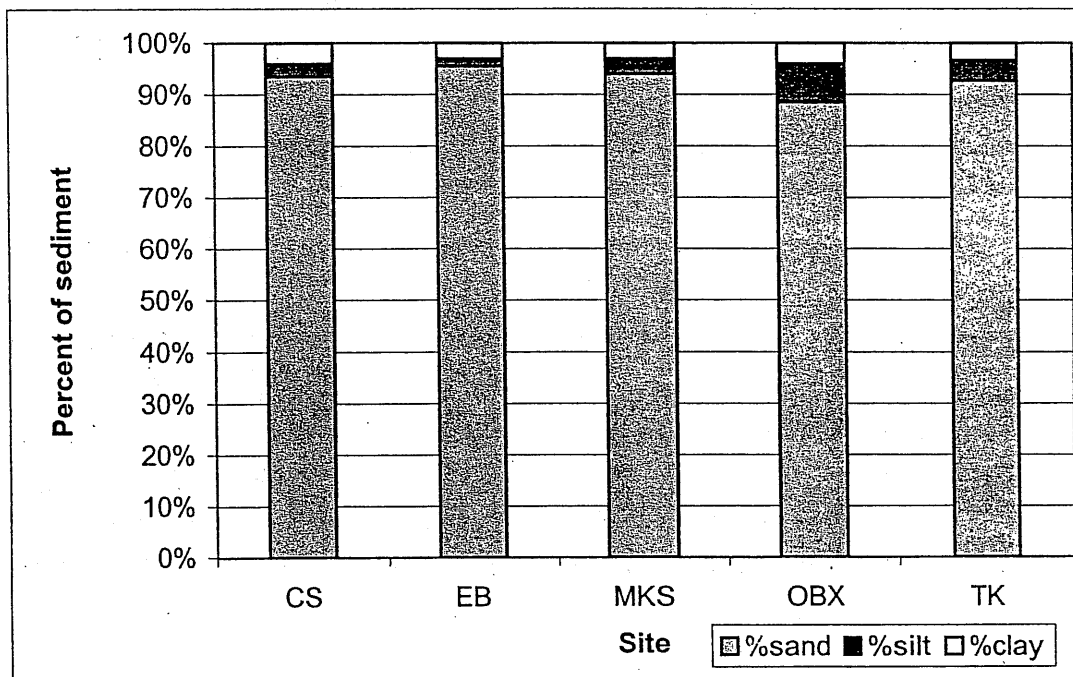


Figure 1.22. Particle size distribution of sediment from the Tahoe Keys East Cove Lagoon (TK), and four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB) Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Because sample sizes were small ($n=2$ or 3), we did not detect differences in particle size according to site, date, or the presence or absence of plants.

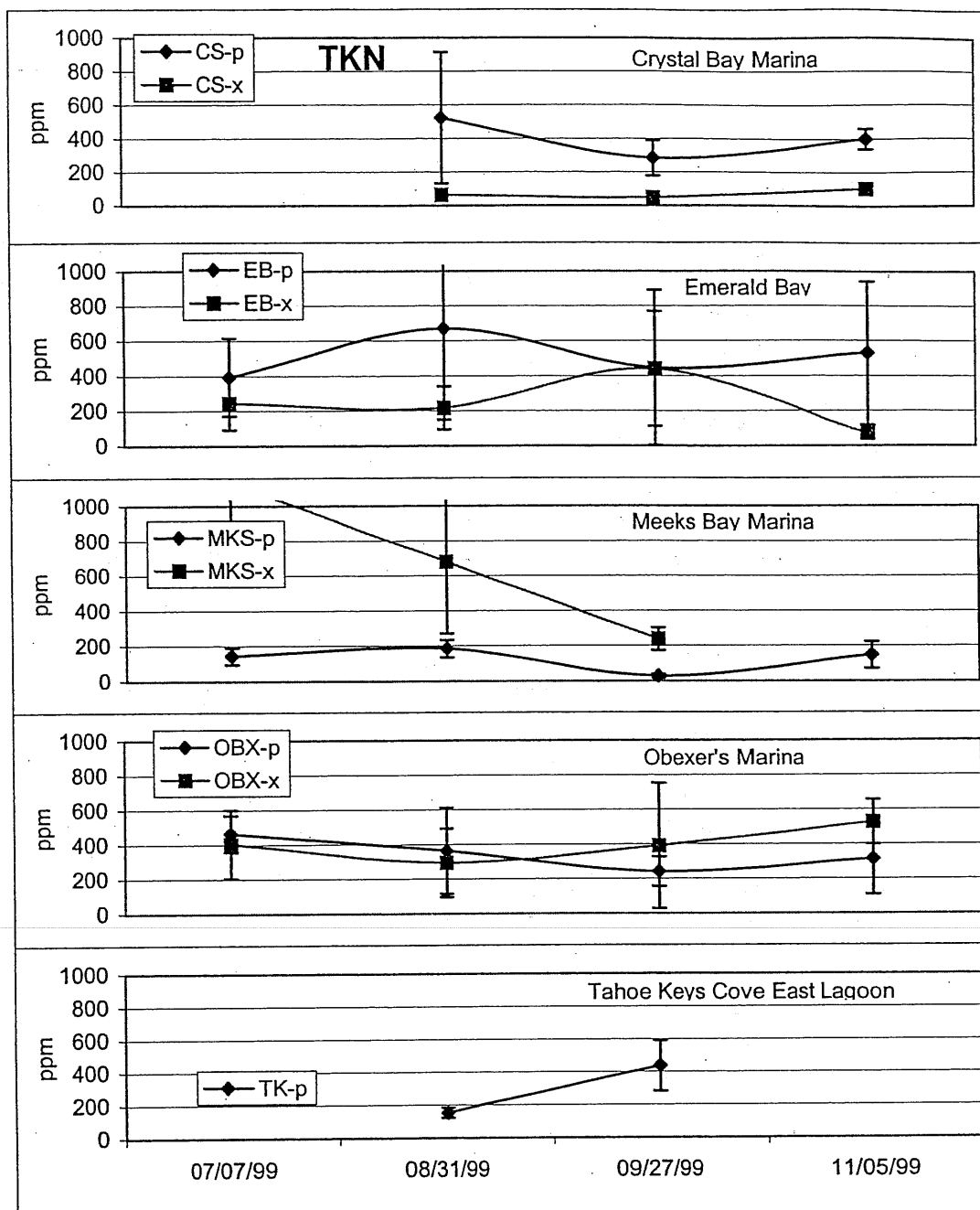


Figure 1.24. Total Kjeldahl nitrogen (TKN) in sediments supporting *M. spicatum* plants (p) and sediments without plants (x) at four Lake Tahoe survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Mean TKN from the Tahoe Keys East Cove Lagoon (TK), the largest source of *M. spicatum* at Lake Tahoe, are given for two survey dates as well. Despite the high variability in TKN (standard error bars), differences due to date, site, and p/x were significant (ANOVA, $F = 8.749_{20,81}$, $p < .0001$). Data were \ln -transformed for statistical analyses, but are presented without transformation in this figure.

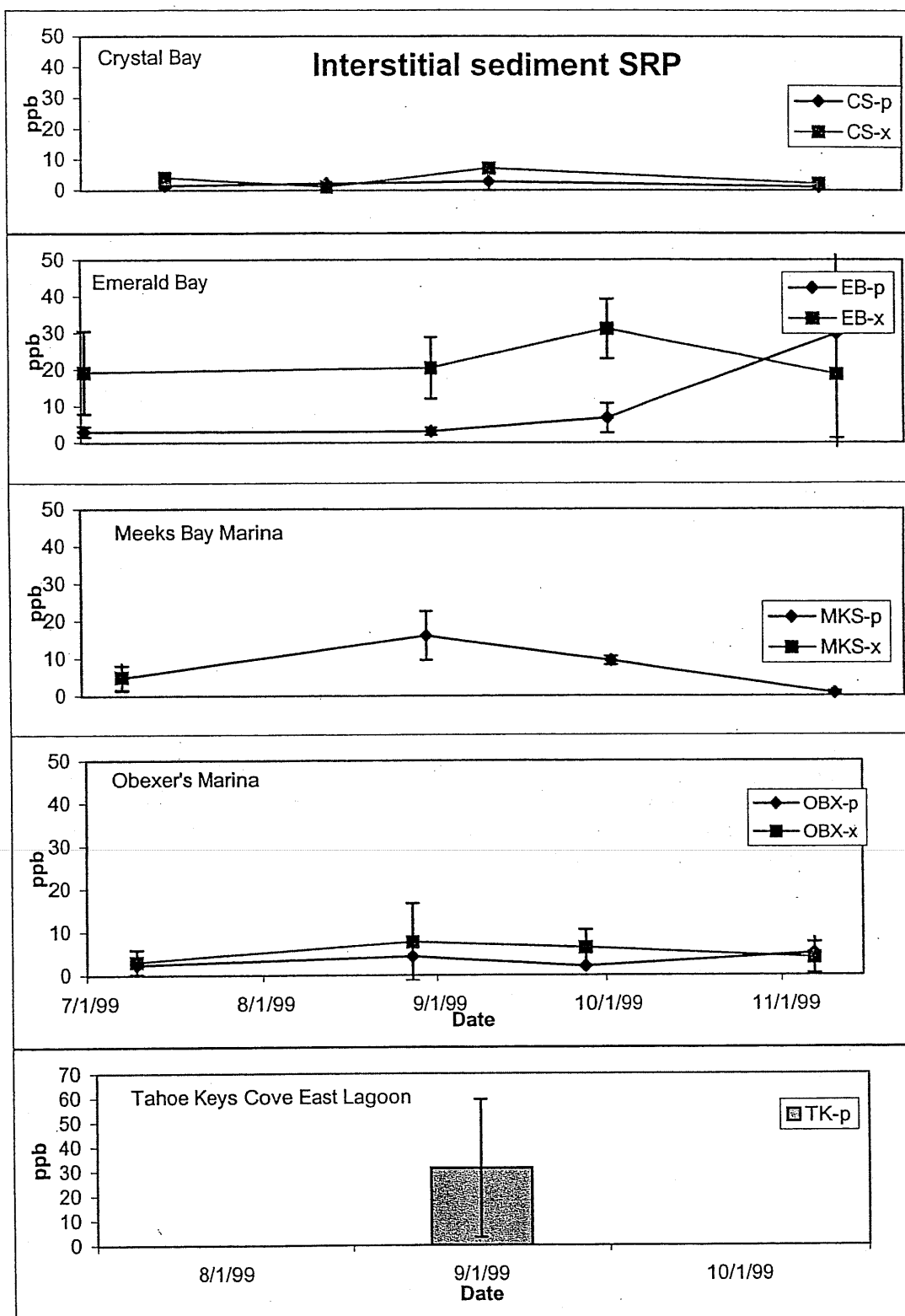


Figure 1.26a. Soluble reactive phosphorus (SRP) varied according to site, date, and the presence or absence of plants (p/x) at four Lake Tahoe sites in summer 1999 (ANOVA, $F = 7.387_{22,64}$, $<.0001$). In general, SRP was low and highly variable.

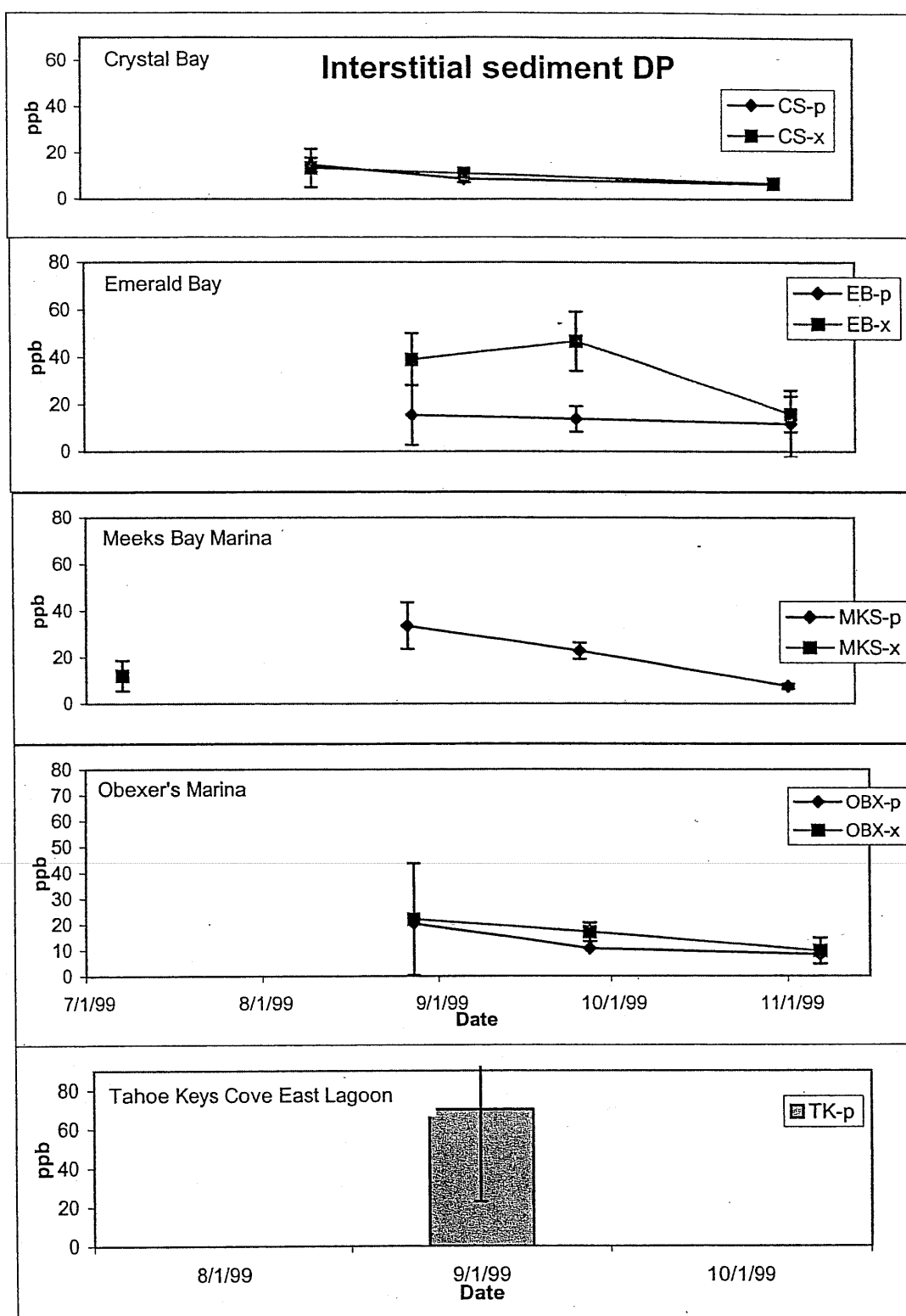


Figure 1.27. Dissolved phosphorus (DP) varied according to site, date, and the presence or absence of plants (p/x) at four Lake Tahoe sites (ANOVA, $F = 6.702_{9,56}$, $<.0001$). Dissolved phosphorus decreased in sediments over time from August 31, 1999 to November 5, 1999, but differences were not due to the presence or absence of plants.

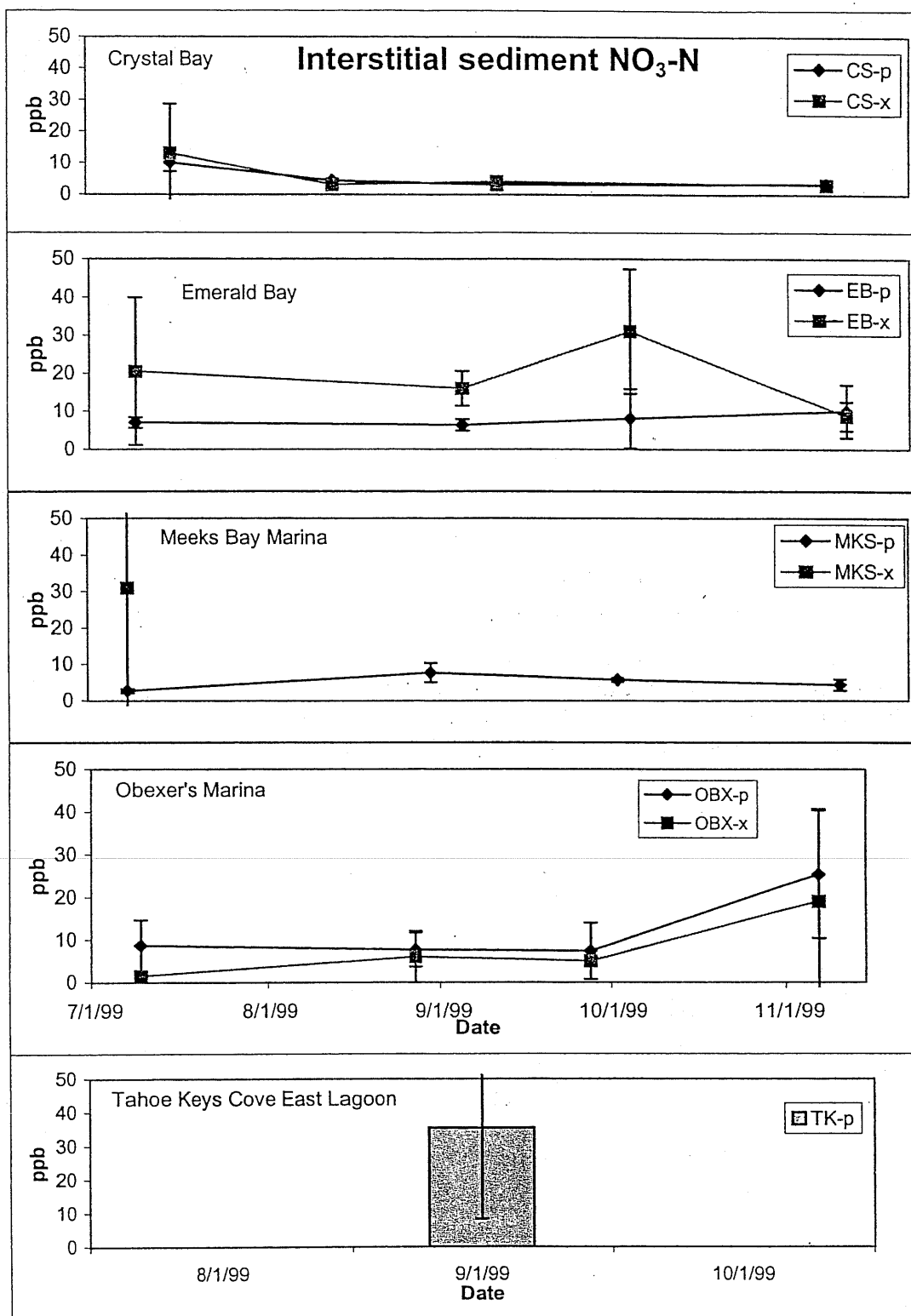


Figure 1.29. Concentrations of NO₃-N varied according to site, date, and the presence or absence of plants (p/x) at four Lake Tahoe sites in summer 1999 (ANOVA, $F = 3.469_{9,64}$, $<.0001$). There were no consistent patterns of NO₃-N in areas of plants and no plants, and among sites, NO₃-N was lowest in sediment at Crystal Bay Marina.

Figure 1.30. Mean survivorship of *M. spicatum* plants grown for 9 weeks under treatment combinations of transplant site, source of *M. spicatum*, and source of sediment in transplant buckets. Reciprocal transplant sites and sources of sediment included the Tahoe Keys Cove East Lagoon (TK), Meeks Bay Marina (MKS), Boatworks Marina (BW), and Caspian Point (RKS). Sites that do not currently have *M. spicatum* populations BW and RKS. *Myriophyllum spicatum* plants used in this experiment were originally from either TK or MKS. *Myriophyllum spicatum* grew successfully at all of the transplant sites except where there was extreme wave action outside of BW.

Figure 1.31. Mean plant height of *M. spicatum* plants grown for 9 weeks under treatment combinations of transplant site, source of *M. spicatum*, and source of sediment in transplant buckets. Reciprocal transplant sites and sources of sediment included the Tahoe Keys Cove East Lagoon (TK), Meeks Bay Marina (MKS), Boatworks Marina (BW), and Caspian Point (RKS). Sites that do not currently have *M. spicatum* populations BW and RKS. *Myriophyllum spicatum* plants used in this experiment were originally from either TK or MKS. *Myriophyllum spicatum* grew successfully at all of the transplant sites except where there was extreme wave action outside of BW. It should be noted that not all treatments had same number of reps for height response variable. Plant heights were averaged among the plants that survived in transplant buckets. Zero's associated with non-survivors have been omitted from this analysis.

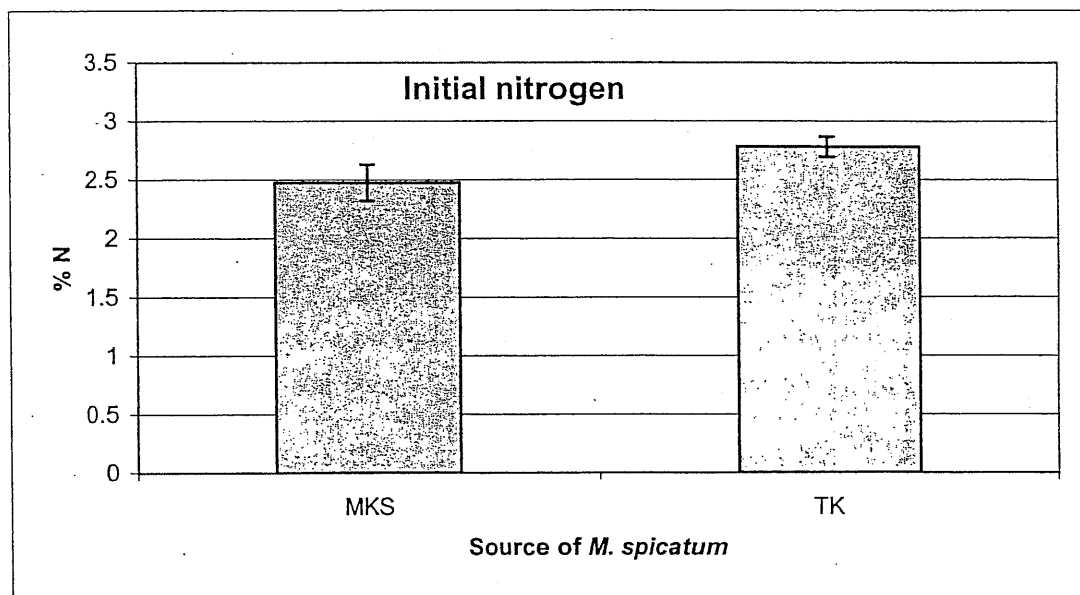


Figure 1.32a. Initial nitrogen concentrations were higher in *M. spicatum* from the Tahoe Keys (TK) than in plants from Meeks Bay (MKS) (ANOVA, $F = 9.162_{1,4}$, $p = .0389$).

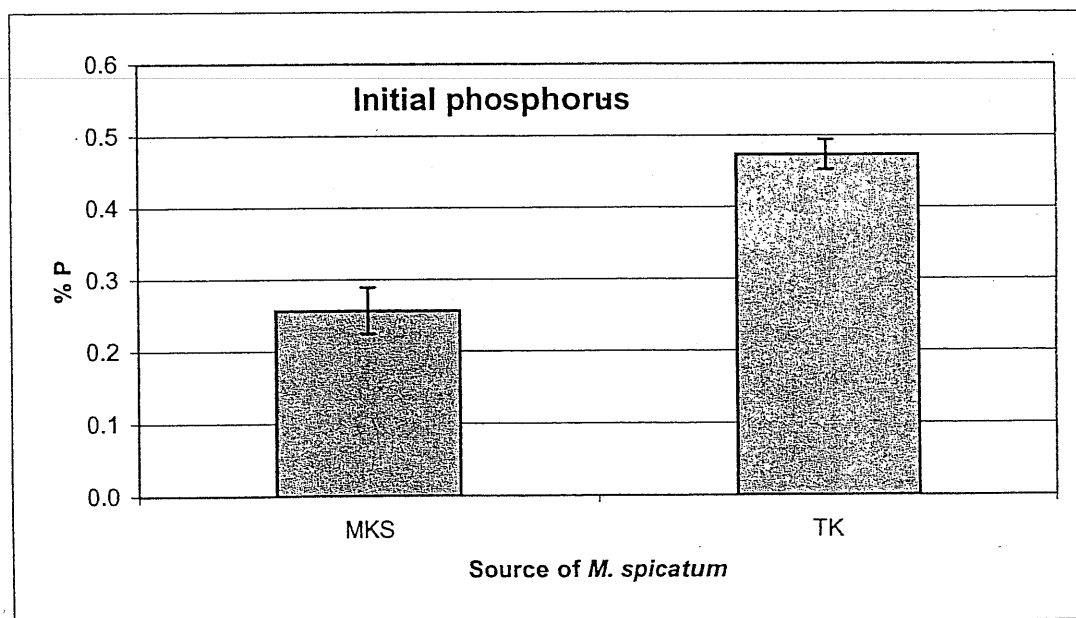


Figure 1.32b. Initial phosphorus concentrations were higher in *M. spicatum* from the Tahoe Keys (TK) than in plants from Meeks Bay (MKS) (ANOVA, $F = 96.022_{1,4}$, $p = .0006$).

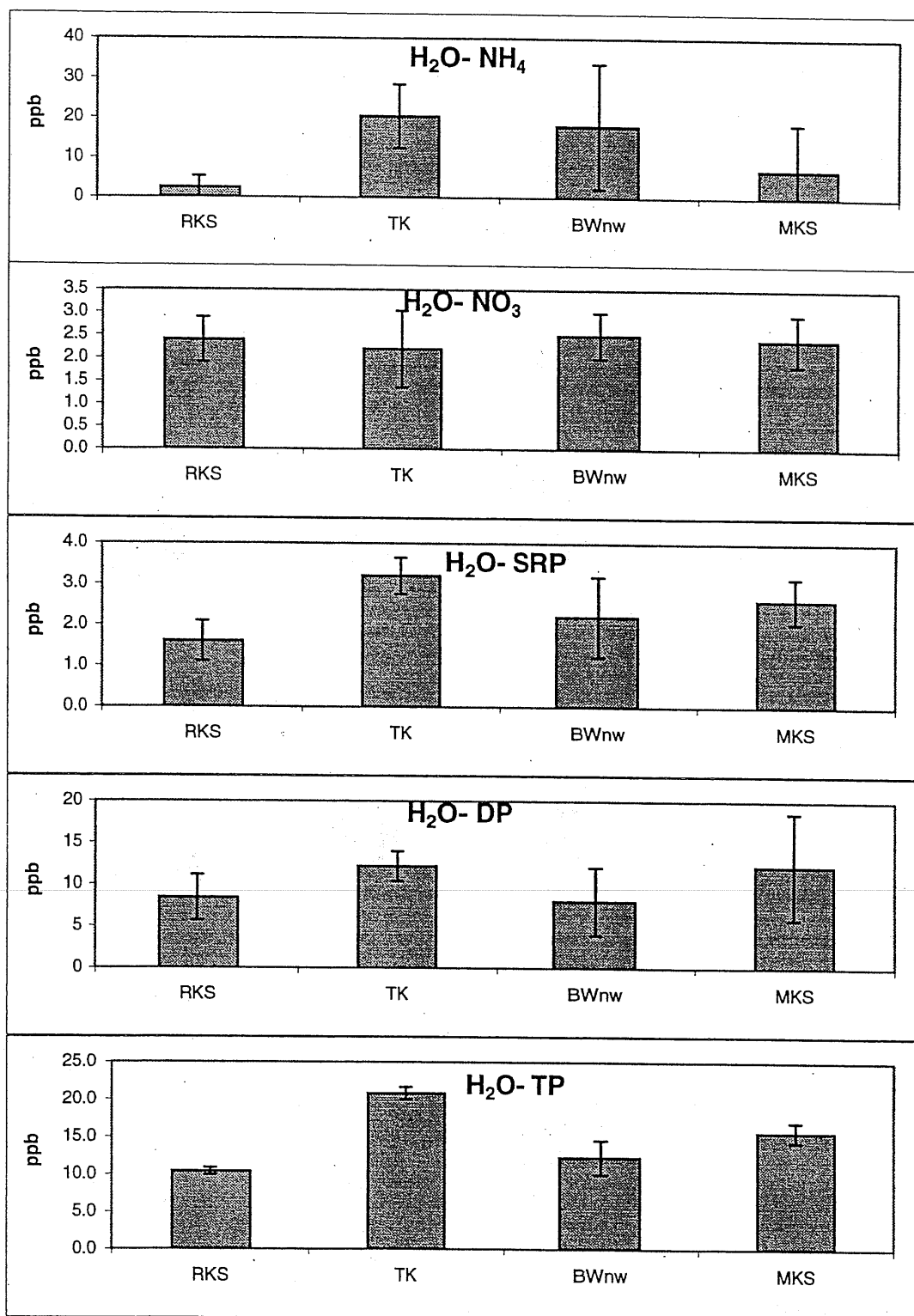


Figure 1.33a. Nutrients ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, SRP, DP, and TP) in lake water collected on August 21, 1999 from transplant sites: Kaspian Point (RKS), Tahoe Keys Cove East Lagoon (TK), Boatworks Marina (BWnw), and Meeks Bay (MKS). Nutrients concentrations are highly variable (standard error bars), but appear to be highest at the Tahoe Keys for all nutrients except $\text{NO}_3\text{-N}$.

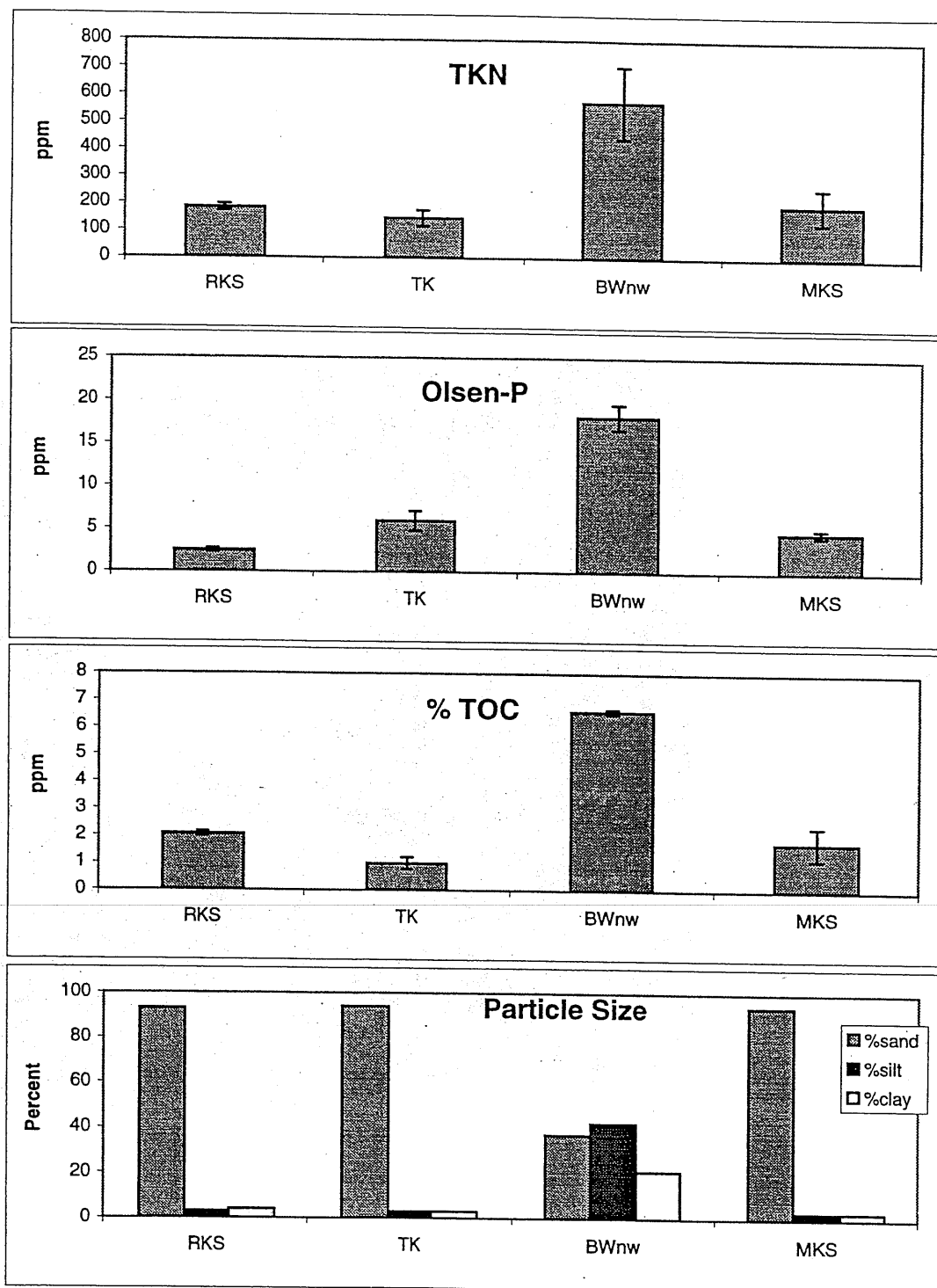


Figure 1.33c. Nutrients (TKN and Olsen-P), organic matter (TOC), and particle size distributions of transplant sediments collected and dried on August 21, 1999 from transplant sites: Kaspian Point (RKS), Tahoe Keys Cove East Lagoon (TK), Boatworks Marina (BWnw), and Meeks Bay (MKS). Sediment from Boatworks Marina appears to have been the most different. It had the highest TKN, Olsen-P and TOC, and the widest distribution of sand, silt and clay. Other sites had lower nutrient contents and were composed primarily of sand.



Figure 2.2. Outdoor sediment-plant microcosms to assess nutrient release from senescing macrophytes, *Myriophyllum spicatum* and *Elodea canadensis*, as well as phytoplankton chlorophyll-*a* response.



Figure 2.4. Daily sampling 1-ml aliquots from stirred water columns of ^{32}P in hydroponic aquatic plant microcosms for liquid scintillation counting.

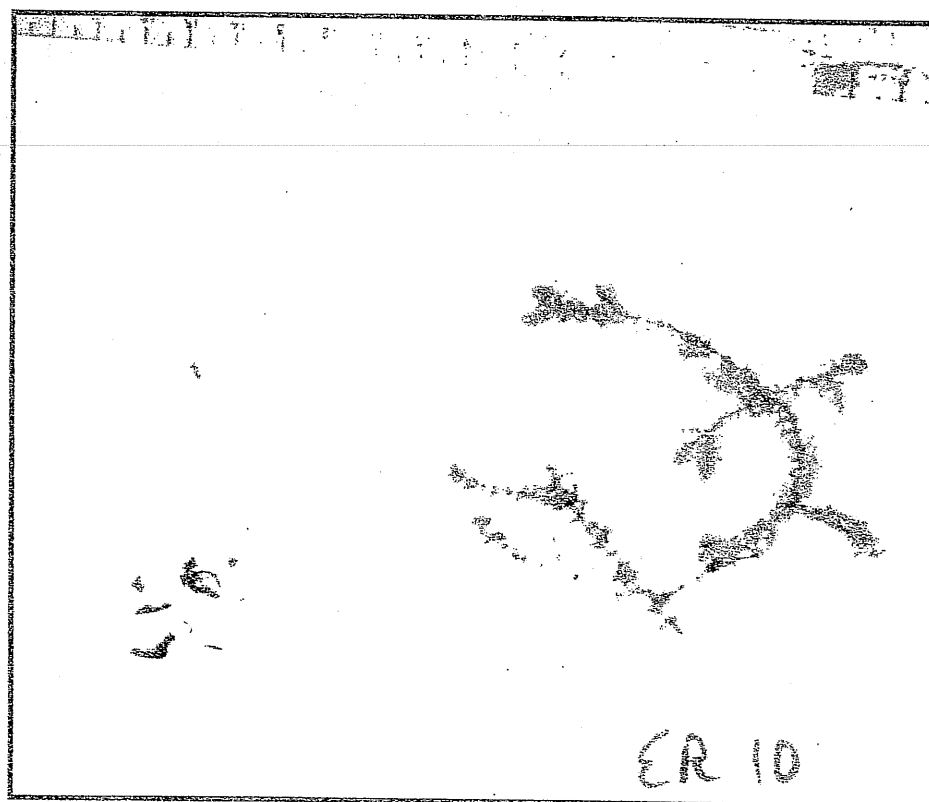
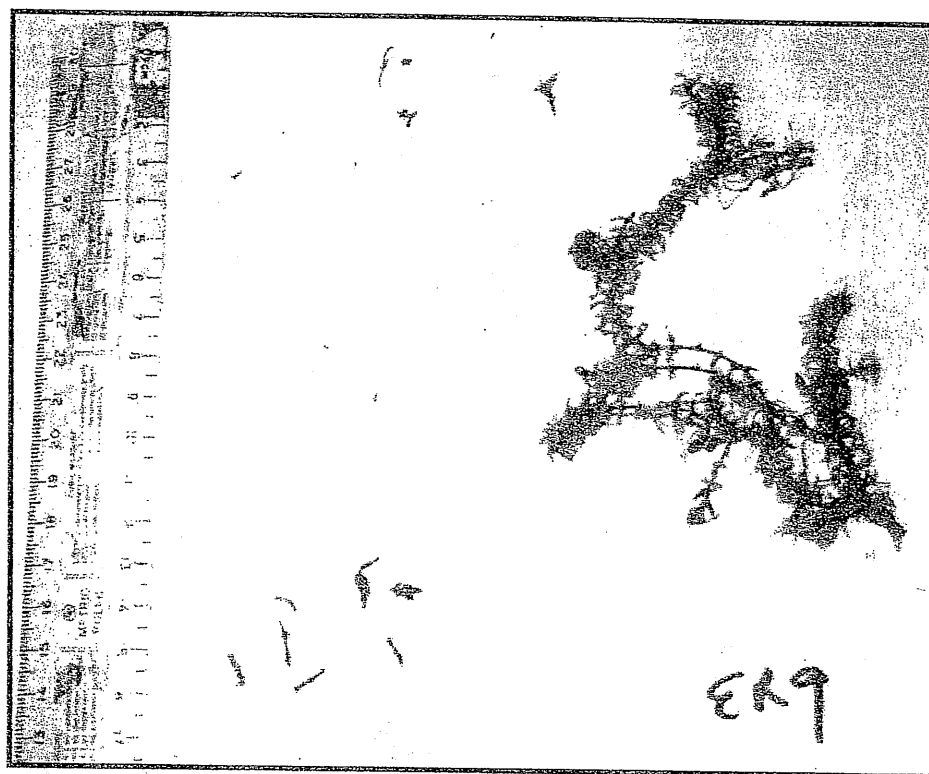


Figure 2.5b. Partially senescent *Elodea canadensis* at the end of the ^{32}P hydroponic aquatic plant microcosm experiment.

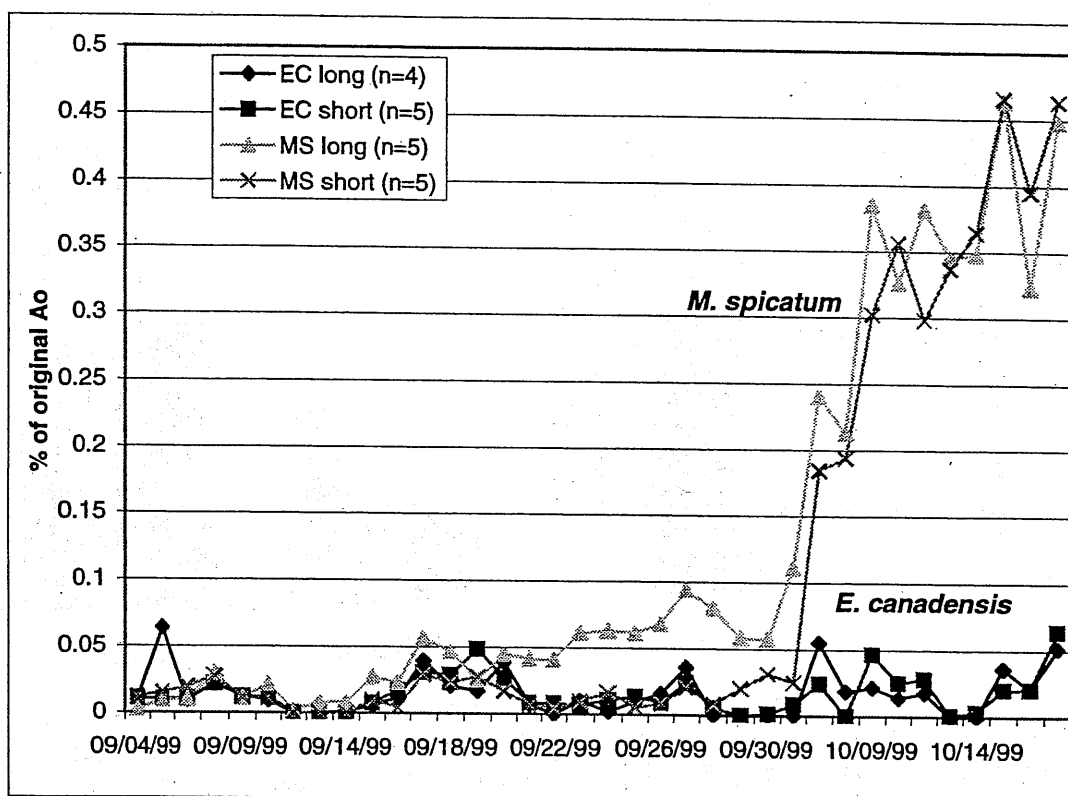


Figure 2.7. ^{32}P detected in water columns of *M. spicatum* (MS) and *E. canadensis* (EC) under long and short-day photoperiods as a percent of the original amount present in sealed root compartments. The pattern of results is the same as in Figure 2.6. ^{32}P activities are higher in MS microcosms over the 45-day experimental period than in EC microcosms.

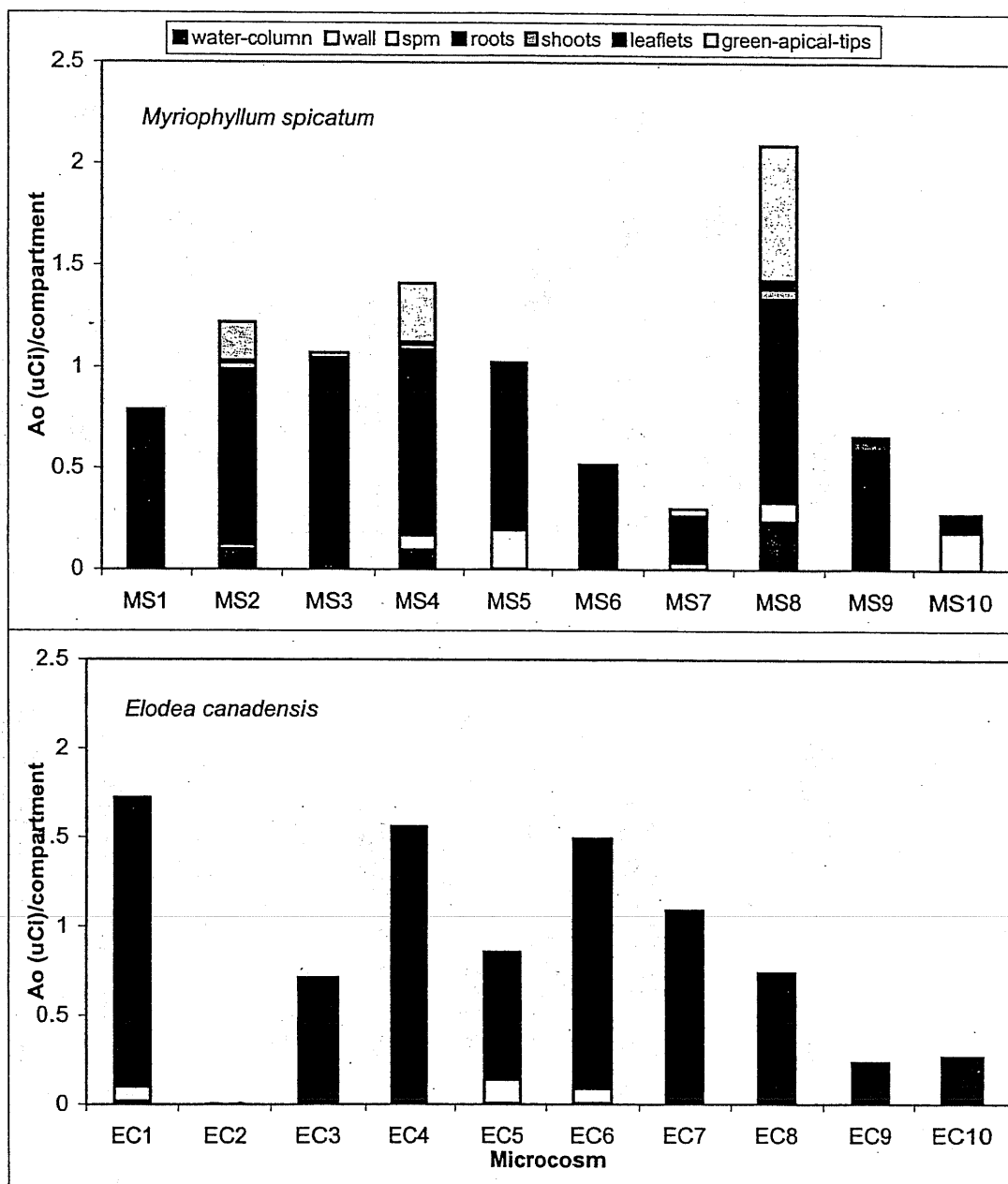


Figure 2.9. ^{32}P activity in biological components of *M. spicatum* (MS) and *E. canadensis* (EC) microcosms at the end of the experiment. Microcosms 1-5 represent long-day treatments for both plant species and microcosms 6-10 had short-day treatments. Suspended particulate matter (SPM) in 20-ml of water from microcosms was collected on filters prior to acid digestion. Biofilm (wall) on side walls of the microcosms were also included in this analysis. Plant parts of MS and EC included roots, shoots, leaflets that had fallen off shoots prior to the final day, and green-apical meristems (3-4cm). Microcosm EC2 has been excluded because it received a double dose of ^{32}P activity at the beginning of the experiment. Among biological components, most of the ^{32}P was detected in plant roots.

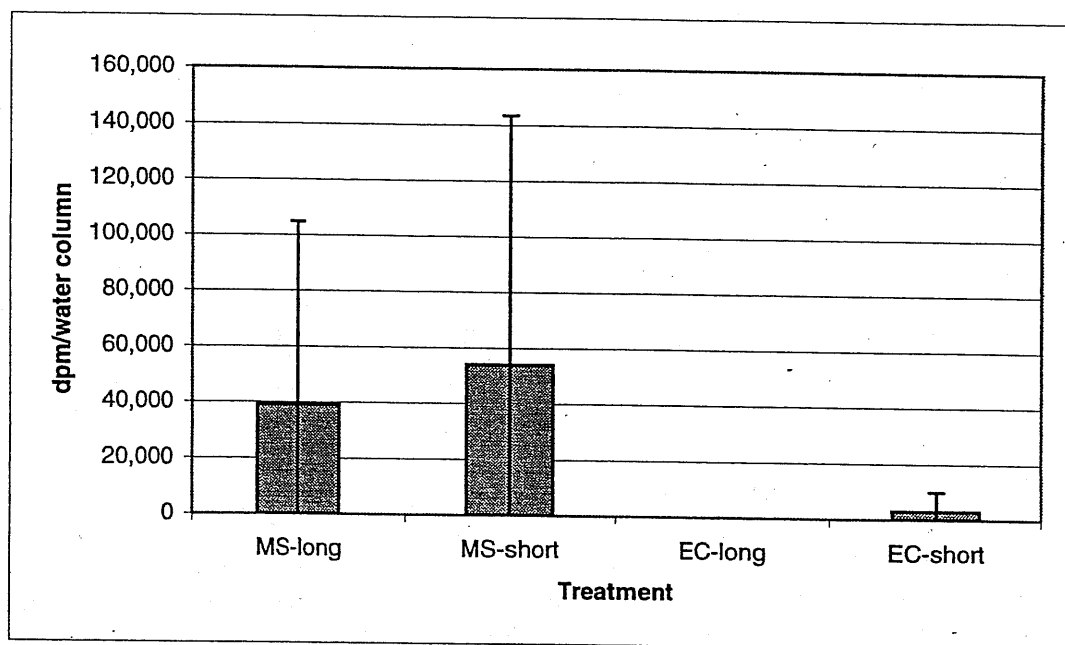


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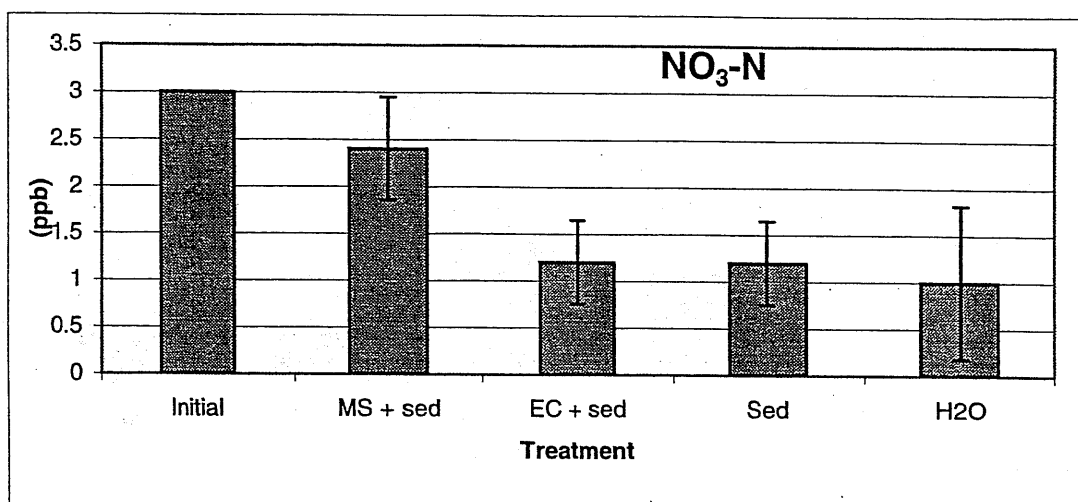


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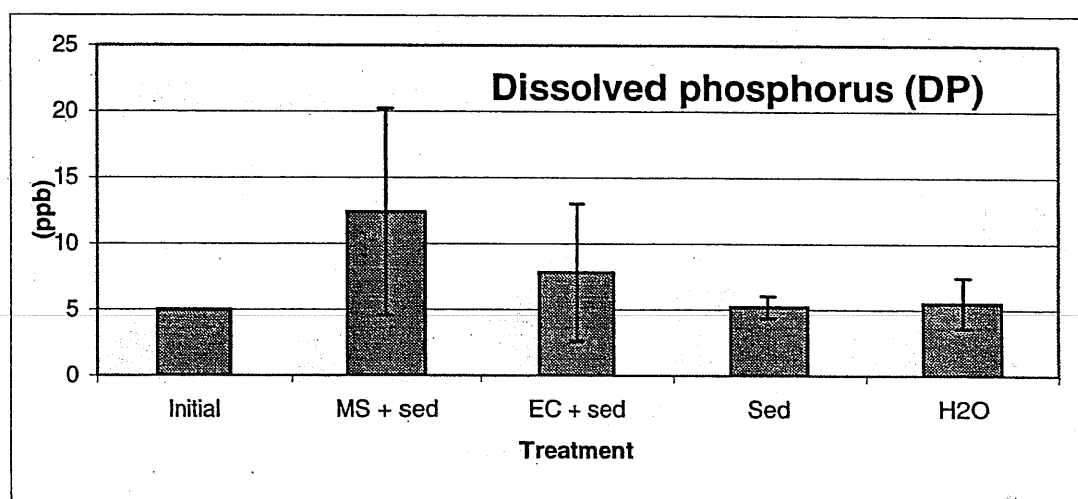


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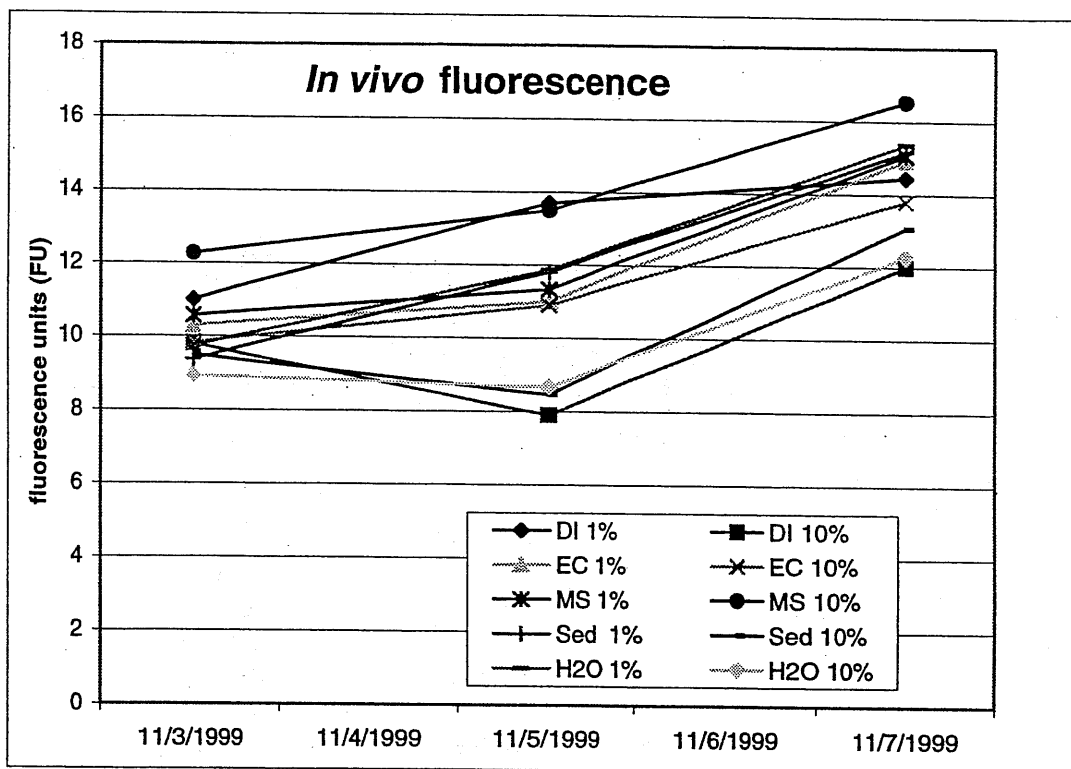


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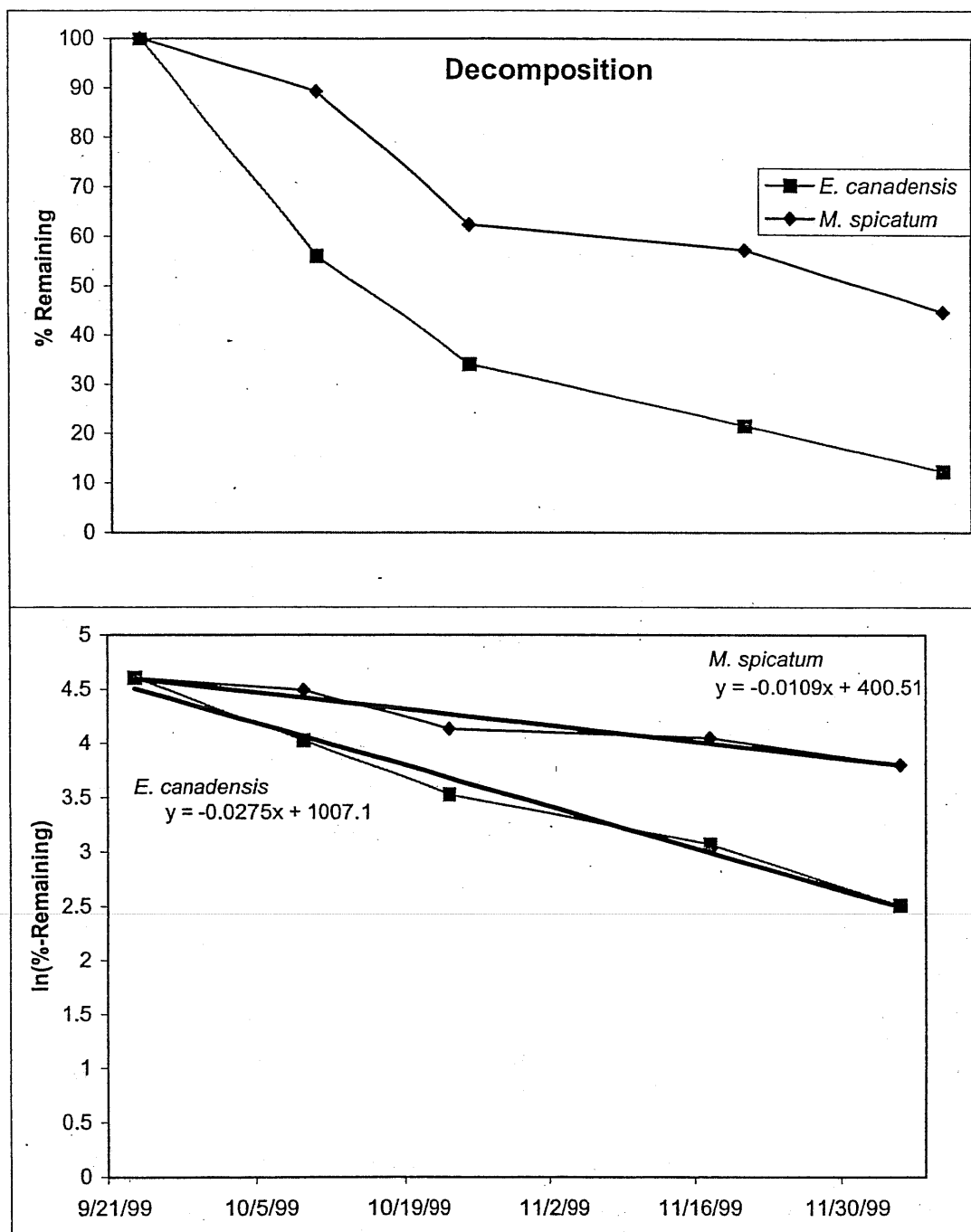


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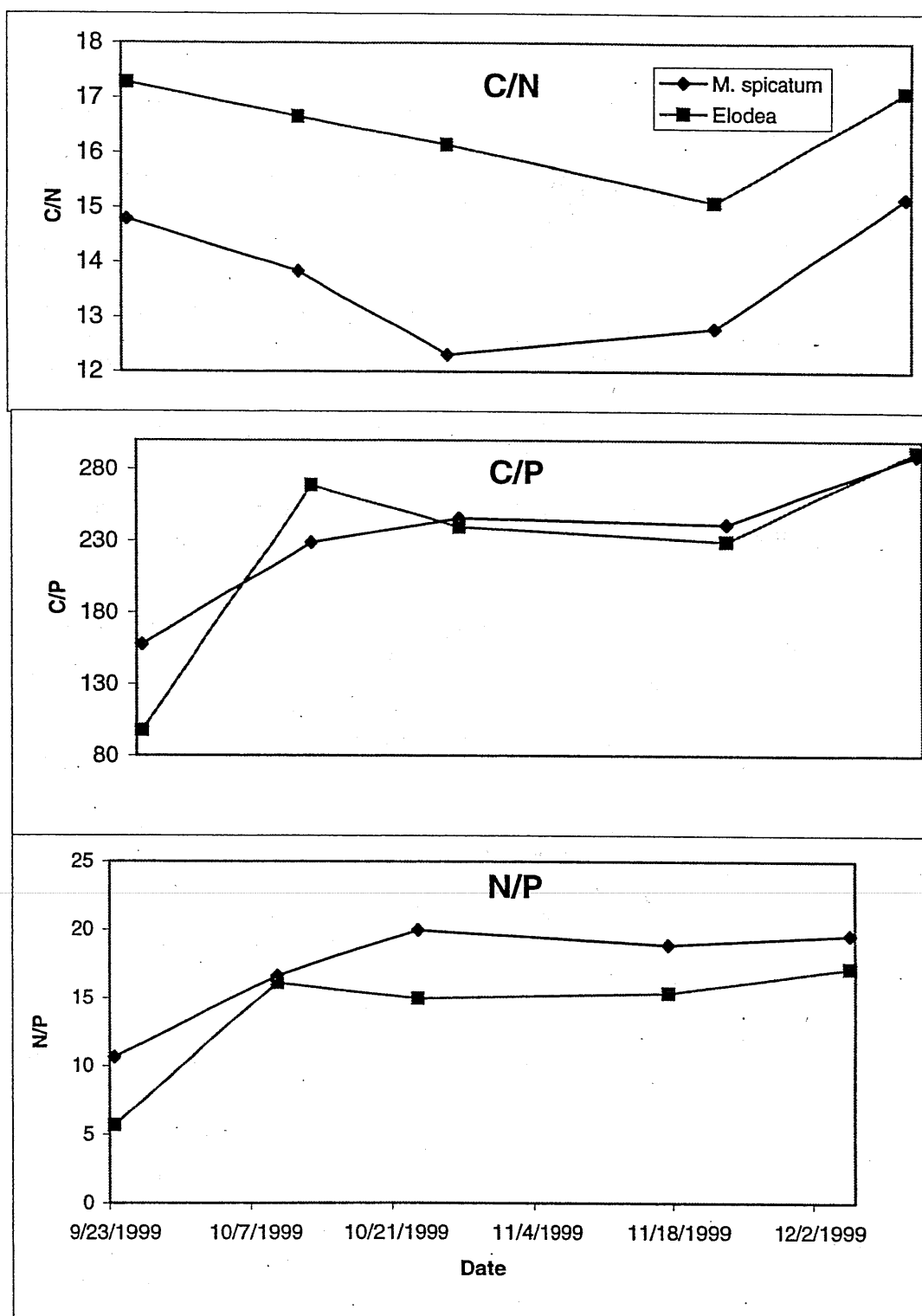


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Table 1.2. Mean height of *M. spicatum* changed according a three-factor ANOVA with interaction and nesting of site, date and the repeated measurement of points along survey transects at four Lake Tahoe locations in Summer 1999. We found significant effects of these factors on plant height (ANOVA, $F=11.277_{51,277}$, $p<.0001$)

Source	DF	F Ratio	p
Date	3	9.1	<0.0001
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Date*Site	9	10.84	<0.0001
Point(Site)	36	7.35	<0.0001

Table 1.4a . Mean C/N ratios for *M. spicatum* plants on four dates during Summer 1999 at four survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Unique combinations of Site and Date affected C/N ratios in plants (ANOVA, $F = 10.457_{14,110}$, $p < .0001$)

Site - Date	Mean C/N	Std Dev
CS - 7/7/99	33.87	10.87
CS - 8/31/99	34.34	7.23
CS - 9/27/99	29.00	12.52
CS - 11/5/99	28.14	8.11
EB - 7/7/99	24.26	7.49
EB - 8/31/99	26.64	7.46
EB - 11/5/99	24.38	8.11
MKS - 7/7/99	16.83	6.56
MKS - 8/31/99	27.21	7.54
MKS - 9/27/99	28.71	6.25
MKS - 11/5/99	20.91	7.59
OBX - 7/7/99	22.43	7.80
OBX - 8/31/99	28.11	7.79
OBX - 9/27/99	35.33	8.42
OBX - 11/5/99	22.42	6.61

Table 1.5a. Mean C/P ratios for *M. spicatum* plants on four dates during Summer 1999 at four survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Unique combinations of Site and Date affected C/P ratios in plants (ANOVA; $F = 103.483_{15,110}$, $p < .0001$)

Site - Date	Mean C/N	Std Dev
CS - 07/07/99	157.639	6.876
CS - 08/31/99	181.215	142.424
CS - 09/27/99	270.113	147.874
CS - 11/05/99	91.157	135.393
EB - 07/07/99	248.272	121.517
EB - 08/31/99	154.514	147.723
EB - 11/05/99	105.692	141.777
MKS - 07/07/99	107.268	43.68
MKS - 08/31/99	116.719	94.022
MKS - 09/27/99	153.69	32.954
MKS - 11/05/99	73.239	86.794
OBX - 07/07/99	146.594	19.106
OBX - 08/31/99	107.597	68.718
OBX - 09/27/99	174.832	53.463
OBX - 11/05/99	95.039	81.077

Table 1.6a. Tuckey-Kramer HSD pairwise contrasts of C/N ratios in plant shoots alone according to Site/Date combinations. Sites consisted of the four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Pairs of means that are significantly different at the $\alpha = 0.05$ level are marked with "**".

	OBX09/27	CS08/31/	CS07/07/	MKS09/27	OBX08/31	MKS08/31	EB08/31/	CS11/05/	EB11/05/	OBX11/05	EB07/07/
OBX09/27											*
CS08/31/					*		*	*	*	*	*
CS07/07/											
MKS09/27											
OBX08/31	*										
MKS08/31	*										
EB08/31/	*										
CS11/05/	*										
EB11/05/	*										
OBX11/05	*										
EB07/07/	*										
CS09/27/	*										
MKS11/05	*										
OBX07/07	*										
MKS07/07	*		*	*	*	*	*	*	*	*	*

Cont.	CS09/27/	MKS11/05	OBX07/07	MKS07/07
OBX09/27	*	*	*	*
CS08/31/	*	*	*	*
CS07/07/				
MKS09/27				
OBX08/31				
MKS08/31				
EB08/31/				
CS11/05/				
EB11/05/				
OBX11/05				
EB07/07/				
CS09/27/				
MKS11/05				
OBX07/07				
MKS07/07				

Table 1.6c. Mean C/N ratios in plant shoots alone according to Site/Date combinations. Sites consisted of the four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Mean C/N in shoots differed by Site*Date ($F = 8.99_{14,58}$, $p < .0001$)

Site*Date	Mean	Std Dev
CS07/07/	24.30	1.00
CS08/31/	28.22	2.35
CS09/27/	17.62	0.73
CS11/05/	20.31	2.19
EB07/07/	17.88	2.86
EB08/31/	20.78	4.21
EB11/05/	18.72	4.47
MKS07/07	11.28	0.24
MKS08/31	21.65	2.68
MKS09/27	23.27	2.89
MKS11/05	16.35	4.01
OBX08/31	21.81	4.55
OBX09/27	28.70	1.37
OBX11/05	18.15	2.44

Table 1.7. Mean C/P ratios in plant shoots alone according to Site/Date combinations. Sites consisted of the four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Mean C/P in shoots differed by Site*Date ($F = 2.401_{14,58}$, $p < .0001$)

Site*Date	Mean	Std Dev
CS07/07/	157.64	6.88
CS08/31/	122.45	81.45
CS09/27/	139.42	23.48
CS11/05/	40.29	47.40
EB07/07/	189.18	34.59
EB08/31/	140.91	114.29
EB11/05/	56.52	63.14
MKS07/07	71.65	8.81
MKS08/31	94.80	63.15
MKS09/27	142.22	28.98
MKS11/05	39.67	53.82
OBX07/07	146.59	19.11
OBX08/31	75.85	38.74
OBX09/27	136.39	12.95
OBX11/05	63.29	52.32

Table 1.9a. Survey date, root/shoot, and sediment and lake water nitrogen species were associated with nitrogen concentrations in *M. spicatum* tissues in the lake surveys (ANOVA, $F = 28.135_{12,129}$, $p < .0001$, $R^2_{adj} = 0.6978$).

Source	DF	Sum of Squares	F Ratio	<i>p</i>
root/shoot	1	24.116	238.755	<.0001
NH4-H2O	1	0.631	6.252	0.0137
NO3-H2O	1	0.401	3.968	0.0485
NH4-sed	1	0.949	9.393	0.0027
NO3-sed	1	0.682	6.751	0.0105
Date	3	1.330	4.388	0.0056
Site	4	1.648	4.080	0.0038

Table 1.9b. Parameter estimates for the effects of sediment and lake water nitrogen on nitrogen concentrations in *M. spicatum* tissues. Negative estimates mean that with every unit of increase of a particular environmental factor, there will be a decrease in the concentration of N in *M. spicatum*.

Parameter Estimates	Estimate	t Ratio	<i>p</i>
NH4-H2O	-0.014	-2.5	0.0137
NO3-H2O	-0.080	-1.99	0.0485
NH4-sed	0.002	3.06	0.0027
NO3-sed	0.020	2.6	0.0105

Table 1.11. Typical Bonferroni pairwise comparisons show differences in chlorophyll-a in lake water according to survey sites, dates, date*site, and date*p/x in Summer 1999, where *p* indicates the presence of plants and *x* indicates areas of surveys sites without plants. Because the sampling regime was not balanced such that every site was sampled on every date, stipulations for comparisons were required in the analysis. Inequality signs indicate whether chlorophyll-a was higher in Column A or B; "-" indicates no significant difference.

Comparison	Stipulation	Column A	Column B	p
Sites	(exclude TK)	CS	< EB	0.0159
		CS	< MKS	0.0002
		CS	- OBX	0.7480
		EB	- MKS	0.2715
		EB	> OBX	0.0074
		MKS	> OBX	0.0001
Sites	(exclude 8/31/99)	TK	> EB	0.0006
		TK	> MKS	0.0034
		TK	> CS	0.0001
		TK	> OBX	0.0001
Site*p/x		CS-p	- CS-x	
		EB-p	- EB-x	0.2233
		MKS-p	> MKS-x	0.0001
		OBX-p	- OBX-x	0.0843
		TK-p	> TK-x	0.0250
Site*Date		MKS-11/5/99	> MKS-7/7/99	0.0326
		OBX-11/5/99	> OBX-7/7/99	0.0055
		OBX-11/5/99	> OBX-8/31/99	0.0003
		OBX-11/5/99	> OBX-9/27/99	0.0666
		OBX-9/27/99	> OBX-8/31/99	0.0645
		CS-11/5/99	- CS-7/7/99	0.1374
		CS-11/5/99	< CS-8/31/99	0.0001
		CS-11/5/99	- CS-9/27/99	0.4077
		CS-7/7/99	> CS-8/31/99	0.0005
		CS-7/7/99	- CS-9/27/99	0.4696
		CS-9/27/99	> CS-8/31/99	0.0001
		TK- no differences among dates		
		EB-no differences among dates		

Table 1.12a. Light extinction coefficients at 1-m depth differed according to date, survey site, and the presence (p) or absence (x) of *M. spicatum* at the four Lake Tahoe survey locations (ANOVA, $F = 8.785_{10,37}$, $p < .0001$). Although p/x was not significant as a main effect, its presence in the site*p/x interaction requires that it remain in the model (Neter et al., 1996).

Source	DF	Sum of Squares	F-Ratio	p
Date	3	0.393	10.307	<.0001
Site	3	0.180	4.715	0.0069
p/x	1	0.000	0.003	0.9604
Site*p/x	3	0.113	2.972	0.0441

Table 1.13a. ANCOVA determined that survey site, date, presence or absence of plants (p/x), and water depth affected the concentration of dissolved oxygen at four survey sites over Summer 1999 ($F = 631.0237_{19,321}$, $p < .0001$). Dissolved oxygen concentrations were nearly saturated in lake water from July 7, 1999 to August 30, 1999, but decreased to 4.95 mg/l by September 27, 1999, the time of plant senescence.

Source	DF	Sum of Squares	F Ratio	p
Date	2	1004.407	5589.842	<.0001
Site	3	7.097	26.332	<.0001
p/x	1	4.542	50.558	<.0001
Depth	1	3.392	37.760	<.0001
Date*Site	6	62.719	116.351	<.0001
Site*p/x	3	9.322	34.588	<.0001
Site*Depth	3	0.877	3.253	0.022

Table 1.14a. Temperatures varied in littoral lake water in areas with and without plants at survey sites by depth, and on different dates (ANCOVA; $F = 275.568_{27,312}$, $p < .0001$). Temperature increased from July 7 ($15.84 \pm 1.20^\circ\text{C}$) to August 31 and September 27, 1999 ($17.36 \pm 0.59^\circ\text{C}$). Temperatures were on average greater in areas with plants than without plants.

Factor	DF	Sum of Squares	F.Ratio	p
site	3	33.633	129.340	<.0001
depth(m)	1	19.542	225.452	<.0001
site*depth(m)	3	2.902	11.161	<.0001
date	2	64.246	370.600	<.0001
date*depth(m)	2	2.516	14.515	<.0001
p/x	1	3.213	37.066	<.0001
site*p/x	3	8.279	31.839	<.0001
date*p/x	2	4.691	27.060	<.0001
site*date	6	79.244	152.372	<.0001
p/x*depth(m)	1	0.464	5.352	0.0214
site*p/x*depth(m)	3	2.642	10.161	<.0001

Table 1.15. Particle size distribution in sediments from the Tahoe Keys Cove East Lagoon (TK) and four lake survey sites: Crystal Bay Marina (CS), Emerald Bay (EB) Meeks Bay Marina (MKS), and Obexer's Marina (OBX). Measurements were made in areas with *M. spicatum* plants (p) and without plants (x). Differences due to site, date, and the presence or absence of plants were not significant. Sample sizes were small (n=2 or 3).

Site	x/p	%Sand	%Silt	%Clay
CS	p	92	4	4
CS	x	95	1	4
EB	p	95	2	3
EB	x	96	1	3
MKS	p	94	3	3
MKS	p	94	3	3
OBX	p	90	6	4
OBX	x	87	9	4
TK	p	94	3	3
TK	p	94	3	3
TK	p	90	6	4

Table 1.17a. ANOVA table for the effects of Site, Date, and the presence (p) or absence (x) of *M. spicatum* plants on Total Kjeldahl Nitrogen (TKN) in survey sediments. There were no constant trends in TKN over time in areas with and without plants.

Factor	DF	F	p
Site	4	3.5	0.011
p/x	1	1.48	0.2269
Site*p/x	3	32.69	0.0001
Date	3	2.67	0.0533
Date*Site	9	4.75	0.0001

Table 1.18a . Olsen-P in dried survey sediments differed according to site, date, and the presence (p) or absence (x) of *M. spicatum* plants (ANOVA, $F = 10.52023,78$, $p < 0.0001$); however, trends were not consistent.

Factor	DF	F	p
Site	4	13.02	0.0001
p/x	1	0.02	0.8953
Site*p/x	3	37.11	0.0001
Date	3	9.45	0.0001
Date*Site	9	5.88	0.0001
Date*p/x	3	3.67	0.0157

Table 1.19a. Soluble reactive phosphorus (SRP) in sediment pore water differed according to survey site, date, and the presence or absence of plants in interstitial sediments (ANOVA, $F = 7.387_{22,64}$, $p < .0001$). Although concentrations were variable, in general, SRP was low in sediment pore water.

Factor	DF	Sum of Squares	F Ratio	p
Date	3	522.406	7.789	0.0002
Site	3	869.051	12.958	<.0001
p/x	1	7.654	0.342	0.5605
Date*Site	9	743.814	3.697	0.0009
Date*p/x	3	338.612	5.049	0.0033
Site*p/x	3	584.773	8.719	<.0001

Table 1.20a. Concentrations of dissolved phosphorus (DP) in interstitial sediments varied by survey site, date, and the presence or absence of plants during the 1999 summer surveys (ANOVA, $F = 6.702_{9,56}$, $p < .0001$). Dissolved phosphorus decreased from August 30 through November 5, but changes were not caused by the presence or absence of plants.

Factor	DF	Sum of Squares	F Ratio	p
Date	2	7.439	11.406	<.0001
Site	3	3.479	3.556	0.0199
p/x	1	0.337	1.035	0.3134
Site*p/x	3	5.355	5.474	0.0023

Table 1.21a. NO₃-N in interstitial sediments varied by survey site, date, and presence or absence of plants in 1999 (ANOVA, $F = 3.46919, 64$, $p < .0001$). In general, NO₃-N in interstitial sediments varied by site, but patterns between areas with and without plants as well as survey dates were not consistent.

Factor	DF	Sum of Squares	F Ratio	p
Date	3	0.290	0.196	0.8987
Site	3	7.598	5.143	0.003
p/x	1	0.691	1.403	0.2406
Date*Site	9	16.282	3.673	0.0009
Site*p/x	3	7.866	5.324	0.0024

Table 1.22a. Logit parameter contrasts for the effects of site, *M. spicatum*-source, and sediment-source on the likelihood of plant survival. Negative estimate numbers are associated with the likelihood of survival. More negative values suggest a lower chance that *M. spicatum* would survive under the parameters of column A than column B. For instance, *M. spicatum* plants would be less likely to survive at Caspian Point than they would in the Tahoe Keys Cove East Lagoon. It should also be noted that due to an unbalanced experimental design, sediment from Caspian Point can only be compared to Tahoe Keys sediment if Tahoe Keys is the only source of *M. spicatum* specified in the model. All site contrasts consider only buckets with *M. spicatum* taken from the Tahoe Keys.

Parameter	Column A	Column B	estimate	Chi-square	p
Site	Boatworks -	Tahoe Keys	-0.884	3.090	0.0788
	Boatworks -	Caspian Point	27.649	44.156	0.0001
	Boatworks -	Meeks Bay	3.771	35.911	0.0001
	Meeks Bay -	Tahoe Keys	-4.780	76.291	0.0001
	Meeks Bay -	Caspian Point	23.878	3.829	0.0504
	Caspian Point -	Tahoe Keys	-28.471	62.388	0.0001
Milfoil-source	Meeks Bay -	Tahoe Keys	-3.045	0.000	0.9854
Sediment-source	Boatworks -	Tahoe Keys	-1.218	4.807	0.0283
	Meeks Bay -	Tahoe Keys	0.071	0.031	0.8602
	Caspian Point -	Tahoe Keys	24.727	3.049	0.0808

Table 1.22b. Parameter estimates for interaction between Site and *M. spicatum*-source. Negative values indicate a lower likelihood of survival. Survivorship was highest among plants grown in their home location. *Myriophyllum spicatum* from the Tahoe Keys had the highest likelihood of survival when it was grown at the Tahoe Keys. The same was true for plants from Meeks Bay Marina. We found that crayfish preferentially grazed plants from foreign locations.

Site	<i>Myriophyllum spicatum</i> Source	
	Meeks Bay	Tahoe Keys
Meeks Bay	6.475	-4.781
Tahoe Keys	-3.430	0

Table 1.24. ANCOVA revealed that NO_3 and SRP from lake water (H_2O) together with interstitial sediment SRP (sed-SRP) and source of *M. spicatum* (MS source) affected plant height over the 9-week growth period of the transplant experiment (ANCOVA, $F = 17.051_{6,123}$, $p < .0001$, $R^2 = 46.1\%$)

Source	DF	Sum of Squares	F-Ratio	p
MS source	1	2059.8084	25.6294	<.0001
$\text{H}_2\text{O}-\text{NO}_3$ *MS source	1	2096.1327	26.0814	<.0001
H_2O -SRP	1	1694.5897	21.0851	<.0001
sed-SRP	1	994.0297	12.3683	0.0006
$\text{H}_2\text{O}-\text{NO}_3$ *sed-SRP	1	838.5599	10.4339	0.0016
$\text{H}_2\text{O}-\text{NO}_3$	1	1591.6245	19.804	<.0001

Table 2.2a. ANOVA results for ^{32}P activity in water of root compartments. Day length was either long or short. Species consisted of *M. spicatum* and *E. canadensis*. Jar refers to the repeated measure of ^{32}P activity in the treatment replicates. Both species took up ^{32}P by the mid-experiment sampling date, September 15, 1999, but had released it again by the end of the experiment. *Elodea canadensis* took up more ^{32}P than *M. spicatum* on September 15, 1999.

Source	DF	F Ratio	p
day length	1	11.122	0.0022
species	1	6.565	0.0153
jar[daylength,species]	15	3.938	0.0006
date	2	292.063	<.0001
day length*date	2	3.978	0.0287
species*date	2	3.374	0.0468

Table 2.3. Mean dry weights and ^{32}P specific activities for the biological compartments (cmpt) of microcosms under treatment combinations of plant species (*M. spicatum* MS vs. *E. canadensis* EC) and photoperiod (short-day vs. long-day) on October 20, 1999. SPM refers to suspended particulate matter in the water.

Microcosm compartment	Treatment	Dry wt. (g)	stdev (g)	Sp. Activity (dpm/g)	stdev (dpm/g)	Sp. Activity (dpm/cmpt)	stdev (dpm/cmpt)
roots	MS-long	0.0094	0.0032	228,065,163	88,461,458	1,926,559	228,422
	MS-short	0.0019	0.0026	822,297,265	388,477,404	1,066,550	785,736
	EC-long	0.0121	0.0087	468,565,257	567,856,127	2,535,004	1,111,987
	EC-short	0.0343	0.0452	92,241,709	117,173,638	1,628,403	1,124,314
shoots	MS-long	0.0580	0.0639	471,994	607,087	25,383	32,501
	MS-short	0.0603	0.0428	710,245	1,524,478	22,662	46,372
	EC-long	0.1757	0.1265	9,719	12,441	2,260	4,289
	EC-short	0.4404	0.3623	398	889	316	707
leaflets	MS-long	0.0307	0.0188	698,427	230,841	22,241	12,070
	MS-short	0.0262	0.0082	2,230,971	3,176,023	45,518	59,873
	EC-long	0.0051	0.0055	0	0	0	0
	EC-short	0.0026	0.0033	0	0	140	314
green tips	MS-long	0.0351	0.0420	2,516,405	3,558,734	222,392	283,687
	MS-short	0.0309	0.0216	16,923,632	23,155,923	312,445	642,310
wall biofilm				(dpm/cm ²)	(dpm/cm ²)		
	MS-long			123	275	83,688	187,133
	MS-short			123	275	80,620	180,271
	EC-long			176	215	118,011	144,230
	EC-short			53	118	35,866	80,200
spm				(dpm/ml)	(dpm/ml)		
	MS-long			228	510	39,058	65,615
	MS-short			509	1,138	53,979	89,476
	EC-long			0	0	0	0
	EC-short			0	0	3,072	6,869

Table 2.5a. Two-way ANOVA of the effects of treatment and date on phytoplankton productivity measured by *in vivo* fluorescence in bioassay flasks over six days. Treatments included exudates in filtered water from microcosms with *M. spicatum*, *E. canadensis*, and no-plant controls at concentration levels of 1% and 10%. According to the model, each of these factors affected the *in vivo* chlorophyll-a response ($F=44.377_{29,51}$, $p<.0001$).

Source	DF	F Ratio	p
Treatment	9	41.2863	<.0001
Date	2	345.753	<.0001
Treatment*date	18	4.7731	<.0001

Table 2.5b. Typical Bonferroni pairwise comparisons of phytoplankton productivity measured by *in vivo* fluorescence at 1% and 10% levels of filtered water from microcosm treatments. Treatments included filtered water from microcosms containing *M. spicatum* (MS), *E. canadensis* (EC), sediment without plants (Sed), lake water without plants or sediment (H2O), and deionized water (DI). Comparisons between Sed and H2O were not significant according to typical Bonferroni. Pairs marked with "***" are not significant using the conservative Bonferroni pairwise analysis.

Pairwise comparison			
treatment		treatment	p
MS 10%	>	MS 1%	<.0001
EC 1%	>	EC 10%	0.0428*
Sed 1%	>	Sed 10%	<.0001
H2O 1%	>	H2O 10%	<.0001
DI 1%	>	DI 10%	<.0001
DI 1%	>	MS 1%	0.0208*
DI 10%	>	EC 10%	<.0001
DI 10%	>	Sed 10%	<.0001
DI 10%	>	H2O 10%	<.0001
DI 10%	>	DI 10%	<.0001
DI 1%	>	EC 1%	0.0025*
EC 10%	>	Sed 10%	<.0001
EC 10%	>	H2O 10%	<.0001
EC 10%	>	DI 10%	0.0001

Table 2.7a. Two-way ANOVA revealed that date, plant species (*M. spicatum* vs. *E. canadensis*), and their interaction affected the amount of decomposition in mesh bags over an 11-week period in Fall, 1999 (ANOVA, $F = 34.325_{9,37}$, $p < .0001$). *Elodea canadensis* decayed faster than *M. spicatum*.

Source	DF	Sum of Squares	F Ratio	p
Date	4	12.112	52.590	<.0001
Plant species	1	4.855	84.331	<.0001
Date*species	4	2.232	9.692	<.0001

Table 2.8a. Harvest date and plant species (*M. spicatum* vs. *E. canadensis*) affected the amount of carbon (% C) remaining in mesh bags following decomposition (ANOVA, $F = 13.886_{5,41}$, $p < .0001$).

Source	DF	Sum of Squares	F Ratio	<i>p</i>
Date	4	176.594	9.708	<.0001
Plant species	1	129.176	28.405	<.0001

Table 2.8b. Parameter estimates for pairwise contrasts for the effects of harvest date and plant species (*M. spicatum* vs. *E. canadensis*) on the amount of carbon (% C) remaining in mesh bags following decomposition.

Parameter Estimates	Estimate	t Ratio	<i>p</i>
Intercept	36.485	116.06	<.0001
Date[09/23/9-12/5/99]	2.015	3.31	0.002
Date[10/09/9-12/5/99]	-2.435	-3.99	0.0003
Date[10/23/9-12/5/99]	-1.485	-2.44	0.0193
Date[11/17/9-12/5/99]	-0.775	-1.27	0.2111
Plant[E. canad.-M.-spic]	-1.660	-5.33	<.0001

Table 2.10a. We found the effects of harvest date and plant species (*M. spicatum* vs. *E. canadensis*) to be significant sources of variation in the amount of phosphorus (% P) remaining in mesh bags following decomposition (ANOVA, $F = 22.289_{9,37}$, $p < .0001$).

Source	DF	Sum of Squares	F Ratio	p
Date	4	5.005856	46.6949	<.0001
Plant species	1	0.0041077	0.1533	0.6977
Date*Plant species	4	0.3813752	3.5575	0.0149

Table 2.10b. Parameter estimates for pairwise contrasts for the effects of harvest date and plant species (*M. spicatum* vs. *E. canadensis*) on the amount of phosphorus (% P) remaining in mesh bags following decomposition. Parameter estimates are on an ln-scale.

Parameter Estimates	Estimate	t Ratio	p
Intercept	-1.787413	-73.89	<.0001
Date[09/23/9-12/5/99]	0.6362508	13.59	<.0001
Date[10/09/9-12/5/99]	-0.195632	-4.18	0.0002
Date[10/23/9-12/5/99]	-0.140484	-3	0.0048
Date[11/17/9-12/5/99]	-0.086983	-1.86	0.0712
Plant[E. canad.--M.-spic]	-0.00947	-0.39	0.6977
Date[09/23/9-12/5/99]*plant[E. canad.--M.-spic]	0.1687018	3.6	0.0009
Date[10/09/9-12/5/99]*plant[E. canad.--M.-spic]	-0.084884	-1.81	0.078
Date[10/23/9-12/5/99]*plant[E. canad.--M.-spic]	-0.038957	-0.83	0.4108
Date[11/17/9-12/5/99]*plant[E. canad.--M.-spic]	-0.008395	-0.18	0.8587

Table 2.12a. We found the effects of harvest date and plant species (*M. spicatum* vs. *E. canadensis*) to be significant sources of variation in the C/P ratio of mesh bag contents following decomposition (ANOVA, $F = 22.2899, 37, p < .0001$).

Source	DF	Sum of Squares	F Ratio	p
Date	4	4.221	34.636	<.0001
Plant species	1	0.056	1.851	0.1819
Date*Plant species	4	0.499	4.098	0.0076

Table 2.12b. Parameter estimates for pairwise contrasts for the effects of harvest date and plant species (*M. spicatum* vs. *E. canadensis*) on the C/P ratio of contents of mesh bags following decomposition. Parameter estimates are on an ln-scale.

Parameter Estimates	Estimate	t Ratio	p
Intercept	5.380	208.6	<.0001
Date[09/23/9-12/5/99]	-0.581	-11.63	<.0001
Date[10/09/9-12/5/99]	0.127	2.55	0.0149
Date[10/23/9-12/5/99]	0.100	2	0.0534
Date[11/17/9-12/5/99]	0.067	1.35	0.185
Plant[E. canad.-M.-spic]	-0.035	-1.36	0.1819
Date[09/23/9-12/5/99]*Plant[E. canad.-M.-spic]	-0.188	-3.77	0.0006
Date[10/09/9-12/5/99]*Plant[E. canad.-M.-spic]	0.113	2.27	0.029
Date[10/23/9-12/5/99]*Plant[E. canad.-M.-spic]	0.023	0.46	0.6477
Date[11/17/9-12/5/99]*Plant[E. canad.-M.-spic]	0.015	0.3	0.7631

Appendix 1.1. Locations of aquatic macrophytes in Lake Tahoe in June, 2000.

Site	Plants	Latitude	Longitude
Tahoe Keys	<i>Myriophyllum spicatum</i>	38.56.00	119.59.53
gas dock	<i>Ceratophyllum demersum</i>		
Outside T. Keys in lake	<i>Ranunculus</i> sp. <i>Myriophyllum</i> sp.	38.56.465	120.00.492
Taylor Creek	plants yet to be sampled	58.56.478	120.03.528
mouth of creek			
Emerald Bay	<i>Potamogeton</i> sp.	58.57.284	120.06.335
northern side	<i>Myriophyllum spicatum</i>		
(Katey's site)	<i>Elodea canadensis</i>		
Emerald Bay	<i>Myriophyllum</i> sp. (<i>verticillatum</i> ? <i>Sibiricum</i> ?)	58.57.187	120.06.374
Viking's home			
Obexer's Marina	<i>Myriophyllum spicatum</i>	39.04.908	120.09.428
	<i>Chara</i> sp.		
Meeks Bay	<i>Myriophyllum spicatum</i>	39.02.195	120.07.399
	<i>Elodea canadensis</i>		
	<i>Utricularia</i> sp.		
	<i>Chara</i> sp.		
	True moss		
	<i>Eleocharis</i> sp.		
Upper Truckee behind dam in lake Tahoe	<i>Myriophyllum spicatum</i>	39.10.048	120.08.605
Crystal Bay	<i>Myriophyllum spicatum</i>	39.14.892	119.58.871
East crib			
Crystal Bay	<i>Myriophyllum spicatum</i>	39.14.902	119.58.941
Middle crib			
Crystal Bay	<i>Myriophyllum spicatum</i>	39.14.910	119.59.056
West crib			
(big hole with no plants in middle of marina)			
Logan Shoals	<i>Myriophyllum spicatum</i>	39.04.206	119.56.584
	<i>Elodea</i> sp.		
Elk Point	<i>Potamogeton foliosa</i>	38.59.031	119.57.362
	<i>Chara</i> sp.		

Appendix 1.2. Total nutrient C, N, and P, as well as C/N, C/P, and N/P ratios for *M. spicatum* roots and shoots during Summer 1999 at four survey sites: Meeks Bay Marina (MKS), Crystal Bay Marina (CS), Emerald Bay (EB), and Obexer's Marina (OBX).

Date	Site	root/shoot	plant%C	plant%N	plant%P	C/N	C/P	N/P
07/07/99	MKS	shoots	35.3	3.16	0.53	11.19	66.60	5.953
07/07/99	MKS	shoots	36.0	3.24	0.44	11.12	81.82	7.355
07/07/99	MKS	shoots	30.6	2.65	0.46	11.54	66.52	5.765
07/07/99	MKS	roots	32.6	1.58	0.30	20.65	108.67	5.263
07/07/99	MKS	roots	34.6	1.29	0.22	26.82	157.27	5.864
07/07/99	MKS	roots	35.8	1.82	0.22	19.66	162.73	8.277
07/07/99	OBX	shoots	37.1	2.33	0.23	15.94	161.30	10.122
07/07/99	OBX	shoots	35.0	2.29	0.28	15.26	125.00	8.193
07/07/99	OBX	shoots	35.3	2.31	0.23	15.26	153.48	10.057
07/07/99	OBX	roots	37.6	1.22		30.77		
07/07/99	OBX	roots	35.9	1.37		26.15		
07/07/99	OBX	roots	37.0	1.19		31.17		
07/07/99	CS	shoots	38.3	1.58	0.24	24.26	159.58	6.579
07/07/99	CS	shoots	39.2	1.68	0.24	23.31	163.33	7.008
07/07/99	CS	shoots	39.0	1.54	0.26	25.36	150.00	5.915
07/07/99	CS	roots	38.6	0.88		44.11		
07/07/99	CS	roots	40.5	0.85		47.65		
07/07/99	CS	roots	36.1	0.93		38.73		
07/07/99	EB	roots	38.3	1.27	0.09	30.21	425.56	14.089
07/07/99	EB	shoots	39.8	1.88	0.23	21.13	173.04	8.191
07/07/99	EB	shoots	41.2	2.51	0.18	16.41	228.89	13.950
07/07/99	EB	shoots	41.4	2.58	0.25	16.06	165.60	10.312
07/07/99	EB	roots	39.1	1.15		33.97		
07/07/99	EB	roots	38.6	1.39		27.69		
08/31/99	MKS	shoots	40.2	2.23	0.26	18.05	154.62	8.565
08/31/99	MKS	shoots	39.6	2.05	0.29	19.28	136.55	7.083
08/31/99	MKS	shoots	39.7	1.57	0.31	25.35	128.06	5.052
08/31/99	MKS	shoots	38.8	1.55	0.35	25.06	110.86	4.423
08/31/99	MKS	shoots	39.6	1.78	0.24	22.23	165.00	7.421
08/31/99	MKS	roots	40.5	1.32	0.18	30.66	225.00	7.339
08/31/99	MKS	roots	38.4	0.99	0.25	38.87	153.60	3.952
08/31/99	MKS	roots	39.4	0.98	0.12	40.04	328.33	8.200
08/31/99	MKS	roots	39.7	1.05		37.81		
08/31/99	MKS-	roots	38.2	1.08		35.24		
08/31/99	OBX	shoots	41.7	2.53	0.47	16.50	88.72	5.377
08/31/99	OBX	shoots	41.7	2.33	0.42	17.90	99.29	5.545
08/31/99	OBX	shoots	40.8	1.72	0.39	23.68	104.62	4.418
08/31/99	OBX	shoots	41.5	2.13	0.38	19.52	109.21	5.595
08/31/99	OBX	roots	38.7	1.34	0.20	28.90	193.50	6.695
08/31/99	OBX	roots	38.0	1.23	0.21	30.82	180.95	5.871
08/31/99	OBX	roots	38.9	1.14	0.19	34.06	204.74	6.011
08/31/99	OBX	roots	38.8	0.96	0.21	40.54	184.76	4.557
08/31/99	CS	roots	35.4	0.77	0.10	45.97	354.00	7.700
08/31/99	CS	roots	40.9	0.91	0.10	44.90	409.00	9.110
08/31/99	CS	shoots	38.8	1.36	0.22	28.57	176.36	6.173
08/31/99	CS	roots	39.1	0.95	0.10	41.07	391.00	9.520

08/31/99	CS	shoots	41.4	1.474	0.19	28.09	217.89	7.758
08/31/99	CS	shoots	40.6	1.474	0.25	27.54	162.40	5.896
11/05/99	CS	roots	38.5	1.154	0.09	33.36	427.78	12.822
11/05/99	CS	roots	39.4	1.124	0.11	35.05	358.18	10.218
11/05/99	CS	roots	40	0.952	0.11	42.02	363.64	8.655
11/05/99	CS	roots	37.8	1.26	0.12	30.00	315.00	10.500
11/05/99	CS	roots	38.9	1.172	0.11	33.19	353.64	10.655
11/05/99	CS	shoots	40.6	1.873	0.22	21.68	184.55	8.514
11/05/99	CS	shoots	40.9	2.197	0.26	18.62	157.31	8.450
11/05/99	CS	shoots	41.4	1.777	0.29	23.30	142.76	6.128
11/05/99	CS	shoots	39.8	1.914	0.27	20.79	147.41	7.089
11/05/99	CS	shoots	40.4	1.986	0.24	20.34	168.33	8.275
08/31/99	EB	roots	39.7	1.394	0.17	28.48	233.53	8.200
08/31/99	EB	roots	39.7	1.616	0.13	24.57	305.38	12.431
08/31/99	EB	roots	38.9	1.317	0.15	29.54	259.33	8.780
08/31/99	EB	shoots	41.9	1.755	0.23	23.87	182.17	7.630
08/31/99	EB	shoots	41.5	2.697	0.17	15.39	244.12	15.865
08/31/99	EB	shoots	41.1	2.505	0.34	16.41	120.88	7.368
11/05/99	EB	roots	44.1	1.185	0.09	37.22	490.00	13.167
11/05/99	EB	roots	43.5	1.309	0.09	33.23	483.33	14.544
11/05/99	EB	roots	41.9	1.599	0.13	26.20	322.31	12.300
11/05/99	EB	shoots	42.9	1.523	0.15	28.17	286.00	10.153
11/05/99	EB	shoots	42	2.364	0.33	17.77	127.27	7.164
11/05/99	EB	shoots	43.2	2.132	0.15	20.26	288.00	14.213
11/05/99	EB	shoots	42.8	2.524	0.18	16.96	237.78	14.022
11/05/99	EB	shoots	42.5	2.833	0.24	15.00	177.08	11.804
08/31/99	MKS	roots	38.7	1.443	0.15	26.82	258.00	9.620
08/31/99	MKS	roots	38.3	1.519	0.24	25.21	159.58	6.329
08/31/99	MKS	shoots	39.5	2.048	0.19	19.29	207.89	10.779
08/31/99	MKS	shoots	38.9	1.823	0.19	21.34	204.74	9.595
08/31/99	MKS	shoots	39.3	1.734	0.28	22.66	140.36	6.193
11/05/99	MKS	roots	38.9	1.874	0.15	20.76	259.33	12.493
11/05/99	MKS	roots	39.6	1.875	0.17	21.12	232.94	11.029
11/05/99	MKS	shoots	39	2.857	0.27	13.65	144.44	10.581
11/05/99	MKS	shoots	35.8	3.32	0.4	10.78	89.50	8.300
11/05/99	MKS	shoots	40.3	2.262	0.2	17.82	201.50	11.310
11/05/99	MKS	shoots	38.3	1.878	0.33	20.39	116.06	5.691
08/31/99	OBX	roots	37.9	1.011	0.18	37.49	210.56	5.617
08/31/99	OBX	roots	38.5	1.112	0.18	34.62	213.89	6.178
08/31/99	OBX	shoots	38.5	1.37	0.29	28.10	132.76	4.724
08/31/99	OBX	shoots	39.3	1.562	0.3	25.16	131.00	5.207
11/05/99	OBX	roots	38.2	1.735	0.28	22.02	136.43	6.196
11/05/99	OBX	shoots	40.6	2.315	0.48	17.54	84.58	4.823
11/05/99	OBX	shoots	39	1.91	0.33	20.42	118.18	5.788

08/31/99	OBX-p	4	27	17	4	
08/31/99	OBX-p	4			7	
08/31/99	OBX-p	2	2			
08/31/99	OBX-x	3	10	14	3	
08/31/99	OBX-x	2	9	5	2	
08/31/99	OBX-x	18	47	25	13	
08/31/99	TK-p	64	106	1488	77	
08/31/99	TK-p	7	99	2000	20	
08/31/99	TK-p	52	89	1822	45	
08/31/99	TK-p	2	3	1953	4	
08/31/99	TK-p	69	89	1818	66	
08/31/99	TK-p	3	8	1245	3	
08/31/99	TK-p	55	129	1112	58	
08/31/99	TK-p	9	38	200	27	
08/31/99	TK-p	21		2481	19	
09/27/99	CS-p	1	9	64	4	
09/27/99	CS-p	1	7	26	4	
09/27/99	CS-p	6	10	142	1	
09/27/99	CS-x	7	11	85	4	
09/27/99	EB-p	2	11	10	4	
09/27/99	EB-p	9	20	28	17	
09/27/99	EB-p	9	10	739	3	
09/27/99	EB-x	33	47	3	35	
09/27/99	EB-x	22	34	25	13	
09/27/99	EB-x	38	59	287	45	
09/27/99	MKS-p	10	19	11	6	
09/27/99	MKS-p	8	26	3	6	
09/27/99	MKS-p	10	23	32	5	
09/27/99	MKS-x	4	11	21	9	
09/27/99	MKS-x	9	19	4	81	
09/27/99	MKS-x	2	6	8	3	
09/27/99	OBX-p	2	11	56	4	
09/27/99	OBX-p	2	10	17	3	
09/27/99	OBX-p	2	11	34	15	
09/27/99	OBX-x	5	16	10	5	
09/27/99	OBX-x	11	21	64	6	
09/27/99	OBX-x	3	14	315	4	
11/05/99	CS-p	1	5	13	3	
11/05/99	CS-p	1	7	15	4	
11/05/99	CS-p	1	7	68	3	
11/05/99	CS-x	2	7	13	3	
11/05/99	CS-x	1	5	7	3	
11/05/99	CS-x	3	8	11	3	
11/05/99	EB-p	1	2	19	5	
11/05/99	EB-p	73	5	739	18	*
11/05/99	EB-p	15	28	127	7	
11/05/99	EB-x	14	24	11	13	
11/05/99	EB-x	4	9	27	6	
11/05/99	MKS-p	1	8	17	4	
11/05/99	MKS-p	1	8	12	3	
11/05/99	MKS-p	0	6	376	6	
11/05/99	OBX-p	2	9	7	10	

Appendix 1.4. Nitrogen and phosphorus in lake water from areas of plants (p) and no plants (x) at four Lake Tahoe Survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). All measurements are in ppb.

Date	Sample	SRP	DP	TP	NH4	NO3
07/07/99	CS-p			13		
07/07/99	CS-p	3			9	3
07/07/99	CS-p	3		11	7	2
07/07/99	CS-p	2		8	0	2
07/07/99	CS-p	3		11	7	26
07/07/99	CS-p	2			2	10
07/07/99	CS-x	2		10	2	8
07/07/99	CS-x	1			4	4
07/07/99	CS-x	3		24	6	5
07/07/99	CS-x	1			3	3
07/07/99	CS-x	2		12	0	2
07/07/99	CS-x			7		
07/07/99	CS-x	1			7	2
07/07/99	CS-x	1				3
07/07/99	EB-p	0			2	1
07/07/99	EB-p	1		10	2	3
07/07/99	EB-p	4			3	4
07/07/99	EB-p	1		10	1	2
07/07/99	EB-p	2		11	2	
07/07/99	EB-p			8		
07/07/99	EB-x			12		
07/07/99	EB-x	1		9	0	1
07/07/99	EB-x	1		11	6	1
07/07/99	EB-x	2		8	7	2
07/07/99	EB-x	1		9	0	3
07/07/99	MKS-p	2		9	1	6
07/07/99	MKS-p	2		9	3	12
07/07/99	MKS-p	3		10	5	7
07/07/99	MKS-p			8		
07/07/99	MKS-p	2		10	2	5
07/07/99	MKS-x	3		31	4	6
07/07/99	MKS-x	3			6	6
07/07/99	MKS-x			17		
07/07/99	MKS-x	4		11	6	8
07/07/99	MKS-x	4		13	3	6
07/07/99	MKS-x					5
07/07/99	OBX-p	3		9	35	4
07/07/99	OBX-p	2		10	4	3
07/07/99	OBX-p			10		
07/07/99	OBX-p	6			4	2
07/07/99	OBX-p			9		
07/07/99	OBX-p	3		15	4	13
07/07/99	OBX-x			8		
07/07/99	OBX-x	1		10	15	2
07/07/99	OBX-x	1		9	1	2
07/07/99	OBX-x	1		10	4	2

09/27/99	CS-x	0	4	6	16	3
09/27/99	CS-x	0	4	6	3	2
09/27/99	CS-x	0	4	7	4	3
09/27/99	CS-x	1	6	5	6	2
09/27/99	CS-x	1	4	8	0	2
09/27/99	EB-p	0	3	9	6	3
09/27/99	EB-p	0	4	7	2	3
09/27/99	EB-p	0	4	8	1	3
09/27/99	EB-p	0	3	9	1	3
09/27/99	EB-p	0	3	8	4	3
09/27/99	EB-x	1	4	6	1	2
09/27/99	EB-x	1	5	9	4	2
09/27/99	EB-x	1	4	6	1	2
09/27/99	EB-x	1	4	7	0	2
09/27/99	EB-x	0	3	9	3	2
09/27/99	MKS-p	3	8	21	3	3
09/27/99	MKS-p	2	9	9	0	2
09/27/99	MKS-p	2	7	18	0	2
09/27/99	MKS-p	5	17	14	0	2
09/27/99	MKS-p	2	6	7	0	2
09/27/99	MKS-x	1	5	7	5	4
09/27/99	MKS-x	1	4	5	20	2
09/27/99	MKS-x	1	4	7	6	2
09/27/99	MKS-x	1	4	6	2	2
09/27/99	MKS-x	1	5	5	21	3
09/27/99	OBX-p	1	6	6	2	2
09/27/99	OBX-p	1	7	5	3	3
09/27/99	OBX-p	1	9	10	1	2
09/27/99	OBX-p	1	6	6	1	2
09/27/99	OBX-p	1	6	6	2	2
09/27/99	OBX-x	3	5	5	1	3
09/27/99	OBX-x	6	7	5	6	2
09/27/99	OBX-x	2	5	5	2	3
09/27/99	OBX-x	1	5	5	1	2
09/27/99	OBX-x	1	6	5	1	2
11/05/99	CS-p	0	5	7	1	3
11/05/99	CS-p	1	6	8	0	2
11/05/99	CS-p	1	7	7	0	2
11/05/99	CS-x	1	3	7	1	2
11/05/99	CS-x	1	4	6	1	2
11/05/99	CS-x	0	5	7	1	2
11/05/99	EB-p	0	3	8	2	2
11/05/99	EB-p	0	3	10	0	3
11/05/99	EB-p	0	3	9	5	2
11/05/99	EB-x	0	3	7	4	2
11/05/99	EB-x	0	3	7	0	2
11/05/99	EB-x	0	3	6	1	2
11/05/99	MKS-p	1	5	7	5	4
11/05/99	MKS-p	1	6	6	10	3
11/05/99	MKS-p	0	5	6	5	3
11/05/99	MKS-p	1	5	6	4	4
11/05/99	MKS-p	0	5	6	7	5

Appendix 1.5. Chlorophyll-a and phaeophytin measured in Lake Tahoe littoral water at four survey sites in the summer of 1999: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX). The Tahoe Keys Cove East Marina (TK) was also sampled on selected dates. Lake water was collected separately from areas with *M. spicatum* plants (p) and without plants (x).

date	Site	p/x	Chl-a	Phaeophytin
07/07/99	CS	p	0.597	0.179
07/07/99	CS	x	-0.019	0.736
07/07/99	CS	p	0.378	0.153
07/07/99	CS	x	0.416	-0.044
07/07/99	CS	x	0.457	-0.101
07/07/99	CS	p	-0.386	1.332
07/07/99	CS	p	0.31	-0.039
07/07/99	CS	x	0.299	0.073
07/07/99	CS	p	14.563	4.425
07/07/99	CS	x	0.363	0.073
07/07/99	CS	p	0.178	0.359
07/07/99	CS	p	0.378	0.472
07/07/99	CS	x	0.333	-0.003
07/07/99	CS	x	0.552	-0.02
07/07/99	EB	p	0.96	-0.774
07/07/99	EB	x	0.998	0.017
07/07/99	EB	x	-0.038	1.26
07/07/99	EB	x	1.002	-0.018
07/07/99	EB	p	5.24	2.861
07/07/99	EB	x	0.692	0.291
07/07/99	EB	p	0.386	0.162
07/07/99	EB	p	0.026	0.202
07/07/99	EB	x	0.8545	-0.0575
07/07/99	EB	p	0.556	0.018
07/07/99	EB	p	0.295	0.183
07/07/99	MKS	p	0.482	0.299
07/07/99	MKS	p	0.582	1.119
07/07/99	MKS	x	1.176	0.892
07/07/99	MKS	x	1.169	10.354
07/07/99	MKS	p	0.73	0.838
07/07/99	MKS	x	0.673	0.645
07/07/99	MKS	p	0.616	0.394
07/07/99	MKS	x	-0.809	2.642
07/07/99	MKS	p	0.506	0.431
07/07/99	MKS	x	-2.207	8.669
07/07/99	MKS	p	0.822	0.7985
07/07/99	MKS	x	1.52	0.633
07/07/99	OBX	p	0.227	0.252
07/07/99	OBX	x	0.265	0.044
07/07/99	OBX	x	0.265	0.282
07/07/99	OBX	x	0.378	-0.064
07/07/99	OBX	p	0.467	-0.092
07/07/99	OBX	x	0.06	0.916
07/07/99	OBX	p	0.348	0.194

09/27/99	EB	p	0.45218	0.230712292
09/27/99	EB	p	0.26126	0.120021974
09/27/99	EB	p	0.348346	0.129678529
09/27/99	OBX	x	0.298104	0.117322292
09/27/99	OBX	x	0.314851	0.106265653
09/27/99	OBX	x	0.331599	0.115126707
09/27/99	OBX	x	0.341647	0.142068262
09/27/99	OBX	x	0.306478	0.106103203
09/27/99	OBX	p	0.348346	0.189431606
09/27/99	OBX	p	0.311502	0.112460519
09/27/99	OBX	p	0.549315	0.324218095
09/27/99	OBX	p	0.616305	0.24869231
09/27/99	MKS	x	0.271308	0.164035837
09/27/99	MKS	x	0.288055	0.147288429
09/27/99	MKS	x	0.355045	0.122979566
09/27/99	MKS	x	0.358395	0.094021623
09/27/99	MKS	x	0.318201	0.128524633
09/27/99	MKS	p	5.392665	4.025557708
09/27/99	MKS	p	0.596208	0.460852661
09/27/99	MKS	p	4.119862	3.107414561
09/27/99	MKS	p	0.880914	0.911678648
09/27/99	MKS	p	0.552664	0.315177844
09/27/99	CS	p	0.561038	0.148885294
09/27/99	CS	p	0.375142	0.105728061
09/27/99	CS	p	0.401938	0.121612978
09/27/99	CS	p	0.408637	0.097841707
09/27/99	CS	p	0.405287	0.115418112
09/27/99	CS	x	0.381841	0.08195679
09/27/99	CS	x	0.442132	0.126945353
09/27/99	CS	x	0.314851	0.072121038
09/27/99	CS	x	0.355045	0.103061874
09/27/99	CS	x	0.38519	0.095679617
09/27/99	TK	x	0.746456	0.413444816
09/27/99	TK	x	0.877086	0.422848605
09/27/99	TK	x	0.845983	0.443382363
09/27/99	TK	p	1.959447	0.709117552
09/27/99	TK	p	1.576888	0.7032812
09/27/99	TK	p	1.897242	0.771322211
11/05/99	TK	x	0.326574	0.317668044
11/05/99	TK	x	0.424547	0.201200708
11/05/99	TK	x	0.402775	0.374014838
11/05/99	TK	p	2.213449	1.485550912
11/05/99	TK	p	2.467451	1.601448558
11/05/99	TK	p	2.540024	1.621351457
11/05/99	MKS	p	0.46809	0.108337447
11/05/99	MKS	p	0.366489	0.077390889
11/05/99	MKS	p	0.489862	0.222195817
11/05/99	MKS	p	0.522519	0.100145871
11/05/99	MKS	p	0.460833	0.131007157
11/05/99	MKS	x	0.322946	0.136346649
11/05/99	MKS	x	0.293917	0.21777799
11/05/99	MKS	x	0.377375	0.186722574

Appendix 1.6. Individual light readings at four Lake Tahoe survey sites: Crystal Bay Marina (CS), Meeks Bay Marina (CS), Emerald Bay (EB), and Obexer's Marina (OBX), and at the Tahoe Keys Cove East Lagoon (TK). Light measurements were taken with a scalar irradiance LiCor except the July readings, for which we used a cosine

Date	Site	x/p	rep	depth(m)	light ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	%-of-surface
07/06/99	CS	p	1	0	18.23	1.00
07/06/99	CS	p	1	0.5	16.5	0.91
07/06/99	CS	p	1	1	14.25	0.78
07/06/99	CS	p	1	1.5	12.2	0.67
07/06/99	CS	p	1	2	11.5	0.63
07/06/99	CS	p	1	2.5	1.8	0.10
07/06/99	CS	p	1	3	0.6	0.03
07/06/99	CS	x	1	0	17.58	1.00
07/06/99	CS	x	1	0.5	14.8	0.84
07/06/99	CS	x	1	1	13	0.74
07/06/99	CS	x	1	1.5	12	0.68
07/06/99	CS	x	1	2	10	0.57
07/06/99	CS	x	1	2.5	9.5	0.54
07/07/99	MKS	p	1	0	16.82	0.99
07/07/99	MKS	p	2	0	17.31	1.01
07/07/99	MKS	p	1	0.5	9.66	0.57
07/07/99	MKS	p	1	1	10.63	0.62
07/07/99	MKS	p	1	1.5	8.73	0.51
07/07/99	MKS	p	1	2	8.71	0.51
07/07/99	MKS	p	1	2.5	5.19	0.30
07/07/99	MKS	p	1	3	6.05	0.35
07/07/99	MKS	p	1	3.5	4.4	0.26
07/07/99	MKS	p	1	4	4.32	0.25
07/07/99	MKS	p	1	4.5	3.31	0.19
07/07/99	MKS	p	1	4.5	2.5	0.15
07/08/99	EB	p	1	0	15.5	1.00
07/08/99	EB	p	1	0.5	12	0.77
07/08/99	EB	p	1	1	10.5	0.68
07/08/99	EB	p	1	1.5	10	0.65
07/08/99	EB	p	1	2	9	0.58
07/08/99	EB	p	1	2.5	6.5	0.42
07/08/99	EB	x	1	0	15.5	1.00
07/08/99	EB	x	1	0.5	13	0.84
07/08/99	EB	x	1	1	12.5	0.81
07/08/99	EB	x	1	1.5	10.5	0.68
07/08/99	EB	x	1	2	9	0.58
07/08/99	EB	x	1	2.5	8	0.52
07/08/99	EB	x	1	3	6	0.39
07/09/99	OBX	p	1	0	14.3	1.00
07/09/99	OBX	p	1	0.5	13.86	0.97
07/09/99	OBX	p	1	1	13.13	0.92
07/09/99	OBX	p	1	1.5	11.6	0.81
07/09/99	OBX	p	1	2	10.4	0.73
07/09/99	OBX	p	1	2.5	3.08	0.22
07/09/99	OBX	x	1	0	15.05	1.00

09/07/99	OBX	p	1	2	1188	0.66
09/07/99	OBX	p	2	2	1282	0.71
09/07/99	OBX	p	3	2	1215	0.68
09/07/99	OBX	p	1	2.3	1108	0.62
09/07/99	OBX	p	2	2.3	1123	0.63
09/07/99	OBX	p	3	2.3	1121	0.62
09/07/99	OBX	x	1	0	1747	1.00
09/07/99	OBX	x	2	0	1738	0.99
09/07/99	OBX	x	3	0	1780	1.01
09/07/99	OBX	x	1	0.5	1836	1.05
09/07/99	OBX	x	2	0.5	1651	0.94
09/07/99	OBX	x	3	0.5	1564	0.89
09/07/99	OBX	x	4	0.5	1663	0.95
09/07/99	OBX	x	1	1	1256	0.72
09/07/99	OBX	x	2	1	1910	1.09
09/07/99	OBX	x	3	1	1476	0.84
09/07/99	OBX	x	4	1	1593	0.91
09/07/99	OBX	x	1	1.5	1432	0.82
09/07/99	OBX	x	2	1.5	1402	0.80
09/07/99	OBX	x	3	1.5	1080	0.62
09/07/99	OBX	x	4	1.5	1555	0.89
09/07/99	OBX	x	1	2	1208	0.69
09/07/99	OBX	x	2	2	1120	0.64
09/07/99	OBX	x	3	2	1301	0.74
09/07/99	OBX	x	4	2	1154	0.66
09/28/99	CS	p	1	0	1753.5	1.05
09/28/99	CS	p	2	0	1685.2	1.01
09/28/99	CS	p	3	0	1564.1	0.94
09/28/99	CS	p	1	0.5	1605.7	0.96
09/28/99	CS	p	2	0.5	1699	1.02
09/28/99	CS	p	3	0.5	1490	0.89
09/28/99	CS	p	1	1	1741.9	1.04
09/28/99	CS	p	2	1	1526.8	0.92
09/28/99	CS	p	3	1	1894	1.14
09/28/99	CS	p	1	1.3	1483.8	0.89
09/28/99	CS	p	2	1.3	894.5	0.54
09/28/99	CS	p	3	1.3	874.9	0.52
09/28/99	CS	p	4	1.3	1511	0.91
09/28/99	CS	x	1	0	1765	0.95
09/28/99	CS	x	2	0	1968	1.06
09/28/99	CS	x	3	0	1828	0.99
09/28/99	CS	x	1	0.5	1888	1.02
09/28/99	CS	x	2	0.5	1455	0.78
09/28/99	CS	x	3	0.5	1607	0.87
09/28/99	CS	x	1	1	1582	0.85
09/28/99	CS	x	2	1	457.5	0.25
09/28/99	CS	x	3	1	1356.9	0.73
09/28/99	CS	x	1	1.5	1318.2	0.71
09/28/99	CS	x	2	1.5	1717.8	0.93
09/28/99	CS	x	3	1.5	971.1	0.52
09/29/99	EB	p	1	0	1769.2	1.14
09/29/99	EB	p	2	0	1434	0.92

09/29/99	OBX	x	2	1	1108	0.65
09/29/99	OBX	x	3	1	1430	0.83
09/29/99	OBX	x	4	1	1486	0.87
09/29/99	OBX	x	1	1.5	1389.9	0.81
09/29/99	OBX	x	2	1.5	1044.6	0.61
09/29/99	OBX	x	3	1.5	930.7	0.54
09/29/99	OBX	x	4	1.5	1285.7	0.75
09/29/99	OBX	x	1	2	421.8	0.25
09/29/99	OBX	x	2	2	996	0.58
09/29/99	OBX	x	3	2	935.3	0.55
09/30/99	OBX	p	1	0	1664	0.99
09/30/99	OBX	p	2	0	1705	1.01
09/30/99	OBX	p	3	0	1688	1.00
09/30/99	OBX	p	1	0.5	1619.8	0.96
09/30/99	OBX	p	2	0.5	1504.2	0.89
09/30/99	OBX	p	3	0.5	1564.6	0.93
09/30/99	OBX	p	1	1	1368.9	0.81
09/30/99	OBX	p	2	1	1529.4	0.91
09/30/99	OBX	p	3	1	1426	0.85
09/30/99	OBX	p	1	1.5	1251.3	0.74
09/30/99	OBX	p	2	1.5	1173.6	0.70
09/30/99	OBX	p	3	1.5	1225.3	0.73
09/30/99	OBX	p	1	2	1189.1	0.71
09/30/99	OBX	p	2	2	1200.4	0.71
09/30/99	OBX	p	3	2	1182	0.70
09/30/99	OBX	p	1	2.4	984.4	0.58
09/30/99	OBX	p	2	2.4	1220.9	0.72
09/30/99	OBX	p	3	2.4	1087.9	0.65
09/30/99	OBX	x	1	0	1751	0.99
09/30/99	OBX	x	2	0	1746	0.99
09/30/99	OBX	x	3	0	1791	1.01
09/30/99	OBX	x	4	0	1777	1.00
09/30/99	OBX	x	5	0	1795	1.01
09/30/99	OBX	x	6	0	1767	1.00
09/30/99	OBX	x	1	0.5	1554	0.88
09/30/99	OBX	x	2	0.5	1742	0.98
09/30/99	OBX	x	3	0.5	1563	0.88
09/30/99	OBX	x	1	1	1783	1.01
09/30/99	OBX	x	2	1	1165	0.66
09/30/99	OBX	x	3	1	1959	1.11
09/30/99	OBX	x	1	1.5	1099	0.62
09/30/99	OBX	x	2	1.5	1380.3	0.78
09/30/99	OBX	x	3	1.5	1257	0.71
09/30/99	OBX	x	1	2	1505	0.85
09/30/99	OBX	x	2	2	1098	0.62
09/30/99	OBX	x	3	2	1509	0.85
09/30/99	OBX	x	4	2	1563	0.88
11/03/99	MKS	p	1	0	494.4	1.02
11/03/99	MKS	p	2	0	490.5	1.01
11/03/99	MKS	p	3	0	472.6	0.97
11/03/99	MKS	p	1	0.5	376.8	0.78
11/03/99	MKS	p	2	0.5	364	0.75

Appendix 1.7. Light extinction coefficients, k , at 1-m depth at Lake Tahoe survey sites in areas with *M. spicatum* plants (p) and without plants (x). Extinction coefficients were calculated by $k = (-\ln(E_z/E_0))/z$, where E_0 is the light at the surface and E_z is the light at depth, z . All measurements were taken in the water column above the plant canopy.

Date	Place	x/p	rep	k
07/07/99	CS	p	1	0.246
07/07/99	CS	x	1	0.302
07/07/99	MKS	p	1	0.473
07/07/99	EB	p	1	0.389
07/07/99	EB	x	1	0.215
07/07/99	OBX	p	1	0.085
07/07/99	OBX	x	1	0.213
09/07/99	MKS	p	1	0.246
09/07/99	MKS	p	2	0.272
09/07/99	MKS	p	3	0.255
09/07/99	MKS	x	1	0.495
09/07/99	MKS	x	2	0.417
09/07/99	MKS	x	3	0.370
09/07/99	MKS	x	4	0.156
09/07/99	OBX	p	1	0.200
09/07/99	OBX	p	2	0.253
09/07/99	OBX	p	3	0.231
09/07/99	OBX	x	1	0.335
09/07/99	OBX	x	2	-0.085
09/07/99	OBX	x	3	0.173
09/07/99	OBX	x	4	0.097
09/29/99	CS	p	1	-0.043
09/29/99	CS	p	2	0.088
09/29/99	CS	p	3	-0.127
09/29/99	CS	x	1	0.159
09/29/99	CS	x	3	0.312
09/29/99	EB	p	1	0.262
09/29/99	EB	p	2	0.228
09/29/99	EB	p	3	0.237
09/29/99	EB	p	1	0.256
09/29/99	EB	p	2	0.179
09/29/99	EB	p	3	0.231
09/29/99	MKS	p	1	0.292
09/29/99	MKS	p	2	0.307
09/29/99	MKS	p	3	0.352
09/29/99	MKS	p	4	0.326
09/29/99	MKS	x	1	0.141
09/29/99	MKS	x	3	0.182
09/29/99	MKS	x	4	0.143
09/29/99	OBX	p	1	0.208
09/29/99	OBX	p	2	0.097
09/29/99	OBX	p	3	0.167
09/29/99	OBX	x	1	-0.006
09/29/99	OBX	x	2	0.419

Appendix 1.8. Individual YSI measurements along a depth profile of dissolved oxygen (DO), temperature, and pH in areas with *M. spicatum* plants (p) and without plants (x) on different dates at four Lake Tahoe survey sites: Crystal Bay Marina (CS), Emerald Bay (EB), Meeks Bay Marina (MKS), and Obexer's Marina (OBX).

Date	Site	p/x	rep	depth(m)	DO%	DO(mg/l)	Temp(oC)	pH
07/07/99	CS	p	1	0		8.47	16.87	7.61
07/07/99	CS	p	2	0		8.9	16.87	7.98
07/07/99	CS	p	3	0		8.39	16.81	7.84
07/07/99	CS	p	4	0		8.39	16.65	7.78
07/07/99	CS	p	5	0		8.47	16.51	7.84
07/07/99	CS	p	1	0.5		8.61	16.87	7.61
07/07/99	CS	p	2	0.5		8.76	16.66	7.92
07/07/99	CS	p	3	0.5		8.52	16.6	7.82
07/07/99	CS	p	4	0.5		8.44	16.66	7.88
07/07/99	CS	p	5	0.5		8.52	16.55	7.84
07/07/99	CS	p	1	1		8.63	16.55	7.61
07/07/99	CS	p	2	1		8.81	16.54	7.9
07/07/99	CS	p	3	1		8.55	16.51	7.82
07/07/99	CS	p	4	1		8.46	16.69	7.89
07/07/99	CS	p	5	1		8.53	16.54	7.86
07/07/99	CS	p	1	1.5		8.64	16.29	7.62
07/07/99	CS	p	2	1.5		8.76	16.5	7.89
07/07/99	CS	p	3	1.5		8.61	16.48	7.83
07/07/99	CS	p	4	1.5		8.46	16.66	7.9
07/07/99	CS	p	5	1.5		8.56	16.55	7.86
07/07/99	CS	p	1	2		8.82	16.32	7.74
07/07/99	CS	p	2	2		8.74	16.51	7.89
07/07/99	CS	p	3	2		8.68	16.44	7.88
07/07/99	CS	p	4	2		8.49	16.53	7.97
07/07/99	CS	p	5	2		8.59	16.44	7.89
07/07/99	CS	x	1	0		7.81	18.41	7.94
07/07/99	CS	x	2	0		7.67	19.7	8
07/07/99	CS	x	3	0		7.55	19.11	8.05
07/07/99	CS	x	4	0		7.02	20.12	8.1
07/07/99	CS	x	5	0		7.58	18.75	8.1
07/07/99	CS	x	1	0.5		8.59	17.7	7.9
07/07/99	CS	x	2	0.5		7.99	18.33	8.08
07/07/99	CS	x	3	0.5		7.91	18.4	8.07
07/07/99	CS	x	4	0.5		7.45	19.04	8.11
07/07/99	CS	x	5	0.5		7.64	18.53	8.12
07/07/99	CS	x	1	1		8.97	17.52	8.09
07/07/99	CS	x	2	1		8.28	17.67	8.15
07/07/99	CS	x	3	1		7.92	17.58	8.13
07/07/99	CS	x	4	1		7.87	18	8.14
07/07/99	CS	x	5	1		7.71	18.14	8.17
07/07/99	CS	x	1	1.5		8.91	17.46	8.18
07/07/99	CS	x	2	1.5		8.41	17.5	8.16
07/07/99	CS	x	3	1.5		7.92	17.76	8.18
07/07/99	CS	x	4	1.5		7.85	17.57	8.18

07/07/99	EB	p	2	0	85.5	8.5	16.33	7.45
07/07/99	EB	p	3	0	84.6	8.46	16.26	7.34
07/07/99	EB	p	4	0	87	8.59	16.18	7.24
07/07/99	EB	p	1	0.5	81.2	8.02	15.95	7.54
07/07/99	EB	p	2	0.5	86.2	8.46	15.84	7.5
07/07/99	EB	p	3	0.5	87.4	8.67	15.92	7.36
07/07/99	EB	p	4	0.5	87.5	8.66	15.86	7.23
07/07/99	EB	p	1	1	81.9	8.08	15.84	7.51
07/07/99	EB	p	2	1	87.6	8.68	15.81	7.5
07/07/99	EB	p	3	1	88	8.7	15.87	7.38
07/07/99	EB	p	4	1	88.1	8.73	15.81	7.27
07/07/99	EB	p	1	1.5	81.8	8.11	15.77	7.49
07/07/99	EB	p	2	1.5	86	8.56	15.68	7.5
07/07/99	EB	p	3	1.5	88.3	8.72	15.93	7.33
07/07/99	EB	p	4	1.5	88.5	8.79	15.75	7.27
07/07/99	EB	p	1	2	81.9	8.16	15.66	7.45
07/07/99	EB	p	2	2	86.1	8.57	15.56	7.5
07/07/99	EB	p	3	2	90.8	9.07	15.43	7.14
07/07/99	EB	x	1	0	88.2	8.59	16.21	7.41
07/07/99	EB	x	2	0	89.3	8.74	15.83	7.36
07/07/99	EB	x	3	0	91.2	9.06	15.88	7.36
07/07/99	EB	x	4	0	89	8.76	16.25	7.37
07/07/99	EB	x	5	0	89.5	8.8	16.23	7.46
07/07/99	EB	x	1	0.5	88.4	8.72	16.33	7.47
07/07/99	EB	x	2	0.5	89.8	8.81	16.38	7.33
07/07/99	EB	x	3	0.5	90.8	8.96	15.89	7.37
07/07/99	EB	x	4	0.5	89.6	8.81	16.17	7.29
07/07/99	EB	x	5	0.5	92.4	9.19	16.15	7.43
07/07/99	EB	x	1	1	89.3	8.87	15.78	7.49
07/07/99	EB	x	2	1	89.5	8.85	16.06	7.33
07/07/99	EB	x	3	1	90.8	9.02	15.62	7.38
07/07/99	EB	x	4	1	91.2	8.99	16.17	7.31
07/07/99	EB	x	5	1	91.9	9.06	15.93	7.47
07/07/99	EB	x	1	1.5	89.5	8.92	15.88	7.5
07/07/99	EB	x	2	1.5	90	8.95	15.6	7.4
07/07/99	EB	x	3	1.5	91.1	9.05	15.54	7.38
07/07/99	EB	x	4	1.5	91.2	9.06	15.91	7.41
07/07/99	EB	x	5	1.5	91.37	9.06	16.12	7.46
07/07/99	EB	x	1	2	89.7	8.92	15.68	7.5
07/07/99	EB	x	2	2	90	8.98	15.5	7.39
07/07/99	EB	x	3	2	91.3	9.08	15.66	7.31
07/07/99	EB	x	4	2	91.3	9.09	15.67	7.43
07/07/99	EB	x	5	2	91.5	9.09	15.78	7.48
07/07/99	OBX	p	1	0	90.7	9	14.6	7.97
07/07/99	OBX	p	2	0	91.5	9.32	14.56	7.75
07/07/99	OBX	p	1	0.5	90	9.23	14.4	7.92
07/07/99	OBX	p	2	0.5	93	9.5	14.46	7.74
07/07/99	OBX	p	1	1	89.6	9.16	14.37	7.9
07/07/99	OBX	p	2	1	92.9	9.31	14.39	7.69
07/07/99	OBX	p	1	1.5	89.2	9.17	14.36	7.86
07/07/99	OBX	p	2	1.5	91.3	9.39	14.37	7.48
07/07/99	OBX	p	1	2	90.8	9.28	14.36	7.8

08/30/99	OBX	x	1	0.5	90.2	8.72	16.96	7.98
08/30/99	OBX	x	2	0.5	89.9	8.65	17.2	7.98
08/30/99	OBX	x	3	0.5	91.2	8.75	17.19	7.94
08/30/99	OBX	x	1	1	90.2	8.71	17.03	7.99
08/30/99	OBX	x	2	1	90.6	8.7	17.2	8.02
08/30/99	OBX	x	3	1	91.3	8.77	17.2	8.04
08/30/99	OBX	x	1	1.5	90.5	8.74	16.99	8
08/30/99	OBX	x	2	1.5	90.4	8.73	17.1	8.04
08/30/99	OBX	x	3	1.5	91.5	8.81	17.19	8.05
08/30/99	OBX	x	1	2	90.8	8.86	16.64	8.04
08/30/99	OBX	x	2	2	92.1	9.08	16.02	8.11
08/30/99	OBX	x	3	2	91.8	9.01	16.24	8.09
08/30/99	OBX	x	1	2.5	91.3	9.01	16.19	8.06
08/30/99	OBX	x	2	2.5	92.6	9.14	15.94	8.1
08/30/99	OBX	x	3	2.5	92.5	9.18	15.84	8.12
08/30/99	CS	p	1	0	95.4	9.03	18.37	8.03
08/30/99	CS	p	2	0	111.8	10.44	18.79	8.14
08/30/99	CS	p	1	0.5	98.5	9.29	18.28	7.95
08/30/99	CS	p	2	0.5	112.2	10.52	18.49	8.09
08/30/99	CS	p	1	1	102.5	9.62	18.12	7.95
08/30/99	CS	p	2	1	112.3	10.52	18.52	8.06
08/30/99	CS	p	1	1.5	102.2	9.67	18.09	7.95
08/30/99	CS	p	2	1.5	112.5	10.52	18.33	8.06
08/30/99	CS	x	1	0	99.1	9.3	18.96	8.12
08/30/99	CS	x	2	0	111	10.97	18.67	7.87
08/30/99	CS	x	1	0.5	101	9.54	18.6	7.92
08/30/99	CS	x	2	0.5	112.1	10.52	18.82	7.95
08/30/99	CS	x	1	1	113.8	10.53	18.4	7.83
08/30/99	CS	x	2	1	113.1	10.6	18.72	7.97
08/30/99	CS	x	1	1.5	111.6	10.45	18.63	7.84
08/30/99	CS	x	2	1.5	111.5	10.48	18.35	7.9
08/30/99	CS	x	1	2	110.8	10.41	18.4	7.85
08/30/99	CS	x	2	2	112.3	10.5	18.34	7.95
08/30/99	EB	p	1	0	89.7	8.47	17.66	7.81
08/30/99	EB	p	2	0	84	8	17.68	7.73
08/30/99	EB	p	1	0.5	88.1	8.36	17.68	7.8
08/30/99	EB	p	2	0.5	90.4	8.3	17.7	7.78
08/30/99	EB	p	1	1	87.7	8.36	17.68	7.81
08/30/99	EB	p	2	1	87	8.29	17.7	7.78
08/30/99	EB	p	1	1.5	87.5	8.34	17.68	7.81
08/30/99	EB	p	2	1.5	87.1	8.31	17.7	7.78
08/30/99	EB	p	1	2	88.9	8.47	17.69	7.79
08/30/99	EB	p	2	2	87.8	8.34	17.68	7.79
08/30/99	EB	p	1	3.5	84.5	8.16	16.99	7.62
08/30/99	EB	p	2	3.5	86.8	8.29	17.5	7.61
08/30/99	EB	x	1	0	91.3	8.66	17.68	7.81
08/30/99	EB	x	1	0.5	90.4	8.6	17.73	7.83
08/30/99	EB	x	1	1	90	8.55	17.73	7.83
08/30/99	EB	x	1	1.5	90	8.55	17.7	7.82
08/30/99	EB	x	1	2	90.4	8.5	17.7	7.82
09/28/99	OBX	p	1	0	52.5	5.08	16.98	7.75
09/28/99	OBX	p	2	0	54.1	5.24	16.93	7.71

09/28/99	EB	p	1	2	46.2	4.38	17.86	7.44
09/28/99	EB	p	1	3	47.2	4.49	17.8	7.42
09/28/99	EB	p	1	3.3	41.2	3.82	17.79	7.2
09/28/99	EB	x	1	0	46.8	4.35	18.57	7.85
09/28/99	EB	x	2	0	52.9	4.9	18.65	7.57
09/28/99	EB	x	1	0.5	47.4	4.41	18.31	7.68
09/28/99	EB	x	2	0.5	53.1	4.97	18.32	7.53
09/28/99	EB	x	1	1	49.5	4.48	18.22	7.63
09/28/99	EB	x	2	1	53	5	18.29	7.52
09/28/99	EB	x	1	1.5	50.1	4.67	18.16	7.51
09/28/99	EB	x	2	1.5	53	5.03	17.92	7.49
09/28/99	EB	x	1	2	50.1	4.73	18.13	7.49
09/28/99	EB	x	2	2	53.5	5.07	17.81	7.44
09/28/99	EB	x	1	3	50.6	4.81	17.79	7.43
09/28/99	EB	x	2	3	52.4	4.97	17.72	7.43
09/28/99	MKS	p	1	0	42.7	4.06	17.71	7.74
09/28/99	MKS	p	2	0	49.4	4.73	17.83	7.47
09/28/99	MKS	p	1	0.5	42.6	4.09	17.38	7.61
09/28/99	MKS	p	2	0.5	49.9	4.79	17.24	7.41
09/28/99	MKS	p	1	1	43.2	4.16	17.41	7.55
09/28/99	MKS	p	2	1	52.3	5.12	16.92	7.33
09/28/99	MKS	p	1	1.5	43.9	4.31	16.18	7.33
09/28/99	MKS	p	2	1.5	53.5	5.23	16.58	7.28
09/28/99	MKS	p	1	2	44.1	4.35	15.95	7.24
09/28/99	MKS	p	2	2	52.3	5.11	16.41	7.2
09/28/99	MKS	x	1	0	47.9	4.49	18.49	7.71
09/28/99	MKS	x	2	0	54.3	5.11	18.43	7.63
09/28/99	MKS	x	1	0.5	48.4	4.58	18.51	7.72
09/28/99	MKS	x	2	0.5	55	5.17	18.37	7.66
09/28/99	MKS	x	1	1	50	4.69	18.53	7.71
09/28/99	MKS	x	2	1	55.2	5.24	17.84	7.68
09/28/99	MKS	x	1	1.5	51.1	4.87	17.56	7.63
09/28/99	MKS	x	2	1.5	55.2	5.32	17.28	7.59
09/28/99	MKS	x	1	2	51.7	4.93	17.21	7.56
09/28/99	MKS	x	2	2	55.2	5.39	16.7	7.51
09/28/99	MKS	x	1	2.5	50.5	4.92	16.61	7.45
09/28/99	MKS	x	2	2.5	57.5	5.61	16.54	7.49

Appendix 1.2. Total nutrient C, N, and P, as well as C/N, C/P, and N/P ratios for *M. spicatum* roots and shoots during Summer 1999 at four survey sites: Meeks Bay Marina (MKS), Crystal Bay Marina (CS), Emerald Bay (EB), and Obexer's Marina (OBX).

Date	Site	root/shoot	plant%C	plant%N	plant%P	C/N	C/P	N/P
07/07/99	MKS	shoots	35.3	3.16	0.53	11.19	66.60	5.953
07/07/99	MKS	shoots	36.0	3.24	0.44	11.12	81.82	7.355
07/07/99	MKS	shoots	30.6	2.65	0.46	11.54	66.52	5.765
07/07/99	MKS	roots	32.6	1.58	0.30	20.65	108.67	5.263
07/07/99	MKS	roots	34.6	1.29	0.22	26.82	157.27	5.864
07/07/99	MKS	roots	35.8	1.82	0.22	19.66	162.73	8.277
07/07/99	OBX	shoots	37.1	2.33	0.23	15.94	161.30	10.122
07/07/99	OBX	shoots	35.0	2.29	0.28	15.26	125.00	8.193
07/07/99	OBX	shoots	35.3	2.31	0.23	15.26	153.48	10.057
07/07/99	OBX	roots	37.6	1.22		30.77		
07/07/99	OBX	roots	35.9	1.37		26.15		
07/07/99	OBX	roots	37.0	1.19		31.17		
07/07/99	CS	shoots	38.3	1.58	0.24	24.26	159.58	6.579
07/07/99	CS	shoots	39.2	1.68	0.24	23.31	163.33	7.008
07/07/99	CS	shoots	39.0	1.54	0.26	25.36	150.00	5.915
07/07/99	CS	roots	38.6	0.88		44.11		
07/07/99	CS	roots	40.5	0.85		47.65		
07/07/99	CS	roots	36.1	0.93		38.73		
07/07/99	EB	roots	38.3	1.27	0.09	30.21	425.56	14.089
07/07/99	EB	shoots	39.8	1.88	0.23	21.13	173.04	8.191
07/07/99	EB	shoots	41.2	2.51	0.18	16.41	228.89	13.950
07/07/99	EB	shoots	41.4	2.58	0.25	16.06	165.60	10.312
07/07/99	EB	roots	39.1	1.15		33.97		
07/07/99	EB	roots	38.6	1.39		27.69		
08/31/99	MKS	shoots	40.2	2.23	0.26	18.05	154.62	8.565
08/31/99	MKS	shoots	39.6	2.05	0.29	19.28	136.55	7.083
08/31/99	MKS	shoots	39.7	1.57	0.31	25.35	128.06	5.052
08/31/99	MKS	shoots	38.8	1.55	0.35	25.06	110.86	4.423
08/31/99	MKS	shoots	39.6	1.78	0.24	22.23	165.00	7.421
08/31/99	MKS	roots	40.5	1.32	0.18	30.66	225.00	7.339
08/31/99	MKS	roots	38.4	0.99	0.25	38.87	153.60	3.952
08/31/99	MKS	roots	39.4	0.98	0.12	40.04	328.33	8.200
08/31/99	MKS	roots	39.7	1.05		37.81		
08/31/99	MKS-	roots	38.2	1.08		35.24		
08/31/99	OBX	shoots	41.7	2.53	0.47	16.50	88.72	5.377
08/31/99	OBX	shoots	41.7	2.33	0.42	17.90	99.29	5.545
08/31/99	OBX	shoots	40.8	1.72	0.39	23.68	104.62	4.418
08/31/99	OBX	shoots	41.5	2.13	0.38	19.52	109.21	5.595
08/31/99	OBX	roots	38.7	1.34	0.20	28.90	193.50	6.695
08/31/99	OBX	roots	38.0	1.23	0.21	30.82	180.95	5.871
08/31/99	OBX	roots	38.9	1.14	0.19	34.06	204.74	6.011
08/31/99	OBX	roots	38.8	0.96	0.21	40.54	184.76	4.557
08/31/99	CS	roots	35.4	0.77	0.10	45.97	354.00	7.700
08/31/99	CS	roots	40.9	0.91	0.10	44.90	409.00	9.110
08/31/99	CS	shoots	38.8	1.36	0.22	28.57	176.36	6.173
08/31/99	CS	roots	39.1	0.95	0.10	41.07	391.00	9.520

08/31/99	CS	shoots	41.4	1.474	0.19	28.09	217.89	7.758
08/31/99	CS	shoots	40.6	1.474	0.25	27.54	162.40	5.896
11/05/99	CS	roots	38.5	1.154	0.09	33.36	427.78	12.822
11/05/99	CS	roots	39.4	1.124	0.11	35.05	358.18	10.218
11/05/99	CS	roots	40	0.952	0.11	42.02	363.64	8.655
11/05/99	CS	roots	37.8	1.26	0.12	30.00	315.00	10.500
11/05/99	CS	roots	38.9	1.172	0.11	33.19	353.64	10.655
11/05/99	CS	shoots	40.6	1.873	0.22	21.68	184.55	8.514
11/05/99	CS	shoots	40.9	2.197	0.26	18.62	157.31	8.450
11/05/99	CS	shoots	41.4	1.777	0.29	23.30	142.76	6.128
11/05/99	CS	shoots	39.8	1.914	0.27	20.79	147.41	7.089
11/05/99	CS	shoots	40.4	1.986	0.24	20.34	168.33	8.275
08/31/99	EB	roots	39.7	1.394	0.17	28.48	233.53	8.200
08/31/99	EB	roots	39.7	1.616	0.13	24.57	305.38	12.431
08/31/99	EB	roots	38.9	1.317	0.15	29.54	259.33	8.780
08/31/99	EB	shoots	41.9	1.755	0.23	23.87	182.17	7.630
08/31/99	EB	shoots	41.5	2.697	0.17	15.39	244.12	15.865
08/31/99	EB	shoots	41.1	2.505	0.34	16.41	120.88	7.368
11/05/99	EB	roots	44.1	1.185	0.09	37.22	490.00	13.167
11/05/99	EB	roots	43.5	1.309	0.09	33.23	483.33	14.544
11/05/99	EB	roots	41.9	1.599	0.13	26.20	322.31	12.300
11/05/99	EB	shoots	42.9	1.523	0.15	28.17	286.00	10.153
11/05/99	EB	shoots	42	2.364	0.33	17.77	127.27	7.164
11/05/99	EB	shoots	43.2	2.132	0.15	20.26	288.00	14.213
11/05/99	EB	shoots	42.8	2.524	0.18	16.96	237.78	14.022
11/05/99	EB	shoots	42.5	2.833	0.24	15.00	177.08	11.804
08/31/99	MKS	roots	38.7	1.443	0.15	26.82	258.00	9.620
08/31/99	MKS	roots	38.3	1.519	0.24	25.21	159.58	6.329
08/31/99	MKS	shoots	39.5	2.048	0.19	19.29	207.89	10.779
08/31/99	MKS	shoots	38.9	1.823	0.19	21.34	204.74	9.595
08/31/99	MKS	shoots	39.3	1.734	0.28	22.66	140.36	6.193
11/05/99	MKS	roots	38.9	1.874	0.15	20.76	259.33	12.493
11/05/99	MKS	roots	39.6	1.875	0.17	21.12	232.94	11.029
11/05/99	MKS	shoots	39	2.857	0.27	13.65	144.44	10.581
11/05/99	MKS	shoots	35.8	3.32	0.4	10.78	89.50	8.300
11/05/99	MKS	shoots	40.3	2.262	0.2	17.82	201.50	11.310
11/05/99	MKS	shoots	38.3	1.878	0.33	20.39	116.06	5.691
08/31/99	OBX	roots	37.9	1.011	0.18	37.49	210.56	5.617
08/31/99	OBX	roots	38.5	1.112	0.18	34.62	213.89	6.178
08/31/99	OBX	shoots	38.5	1.37	0.29	28.10	132.76	4.724
08/31/99	OBX	shoots	39.3	1.562	0.3	25.16	131.00	5.207
11/05/99	OBX	roots	38.2	1.735	0.28	22.02	136.43	6.196
11/05/99	OBX	shoots	40.6	2.315	0.48	17.54	84.58	4.823
11/05/99	OBX	shoots	39	1.91	0.33	20.42	118.18	5.788

Site	MS	Sed	HT	H2O-NH4	H2O DP	H2O SRP	H2O NO3	H2O TP	H2O Chl-a	sed NH4	sed DP	sed SRP	sed NO3	TKN	P-olsen	% TOC	% sand	% silt	% clay
			cm	ppb	ppb	ppb	ppb	ppb	ug/ml	ppb	ppb	ppb	ppb	ppm	ppm				
BW	TK	TK	17	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	26	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	42	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	19	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	21	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	29	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	23	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	14	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	26	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	23	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	17	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	30	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	24	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	21	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	26	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	2	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	27	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	TK	22	18	8	2.2	2.5	12.3	0.555	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
BW	TK	BW	23	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	26	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	22	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	23	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	21	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	26	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	12	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	24	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	18	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	23	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
BW	TK	BW	13	18	8	2.2	2.5	12.3	0.555	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	TK	40	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	TK	TK	17	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	TK	TK	30	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3

Site	MS	Sed	HT	H2O-NH4	H2O DP	H2O SRP	H2O NO3	H2O TP	H2O Chl-a	sed NH4	sed DP	sed SRP	sed NO3	TKN	P-olsen	% TOC	% sand	% silt	% clay
TK	MKS	TK	43	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	MKS	TK	40	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	MKS	TK	21	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	MKS	TK	16	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	MKS	TK	40	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	MKS	TK	19	20.4	12.2	3.2	2.2	20.8	2.522	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
TK	MKS	MKS	21	20.4	12.2	3.2	2.2	20.8	2.522	46.8	34.6	17.8	7	195	4.6	1.758	94	3	3
TK	MKS	MKS	22	20.4	12.2	3.2	2.2	20.8	2.522	46.8	34.6	17.8	7	195	4.6	1.758	94	3	3
TK	MKS	MKS	25	20.4	12.2	3.2	2.2	20.8	2.522	46.8	34.6	17.8	7	195	4.6	1.758	94	3	3
TK	MKS	MKS	21	20.4	12.2	3.2	2.2	20.8	2.522	46.8	34.6	17.8	7	195	4.6	1.758	94	3	3
TK	MKS	MKS	18	20.4	12.2	3.2	2.2	20.8	2.522	46.8	34.6	17.8	7	195	4.6	1.758	94	3	3
TK	MKS	MKS	14	20.4	12.2	3.2	2.2	20.8	2.522	46.8	34.6	17.8	7	195	4.6	1.758	94	3	3
TK	TK	BW	59	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	46	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	32	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	55	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	43	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	35	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	33	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	26	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	38	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	26	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	37	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	43	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	34	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	24	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	26	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	21	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
TK	TK	BW	15	20.4	12.2	3.2	2.2	20.8	2.522	62.2	46	38	20	573.3	18.1	6.604	37	42	21
MKS	TK	TK	19	7	12.2	2.6	2.4	15.6	0.622	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
MKS	TK	TK	0	7	12.2	2.6	2.4	15.6	0.622	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
MKS	TK	TK	0	7	12.2	2.6	2.4	15.6	0.622	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3
MKS	TK	TK	23	7	12.2	2.6	2.4	15.6	0.622	1570.9	74.9	59.4	34.1	146.7	6	0.993	94	3	3

Appendix 2.1. Mean 32P activities detected in the water columns of *M. spicatum* (MS) and *E. canadensis* (EC) microcosms under long and short-day photoperiods. Activities were also transformed to a percent of the starting activity in the root compartment of mason jars.

Date	Treatment	Mean Ao (dpm)	Std. Dev. Ao (dpm)	Percent of start	Std. Dev. % of start
09/04/1999	EC-long	2783	3552	0.0112	0.0143
09/05/1999	EC-long	15893	28112	0.0637	0.1124
09/07/1999	EC-long	2319	1527	0.0095	0.0063
09/08/1999	EC-long	5383	3624	0.0218	0.0145
09/09/1999	EC-long	3180	3760	0.0128	0.0151
09/10/1999	EC-long	2368	4017	0.0095	0.0162
09/11/1999	EC-long	0	0	0.0000	0.0000
09/13/1999	EC-long	0	0	0.0000	0.0000
09/14/1999	EC-long	268	535	0.0011	0.0022
09/15/1999	EC-long	1471	835	0.0060	0.0033
09/16/1999	EC-long	2886	5416	0.0116	0.0218
09/17/1999	EC-long	9720	4668	0.0394	0.0184
09/18/1999	EC-long	5078	2296	0.0207	0.0093
09/19/1999	EC-long	4198	1819	0.0170	0.0072
09/20/1999	EC-long	9500	5171	0.0390	0.0214
09/21/1999	EC-long	1768	3535	0.0071	0.0143
09/22/1999	EC-long	0	0	0.0000	0.0000
09/23/1999	EC-long	2475	4950	0.0100	0.0200
09/24/1999	EC-long	495	990	0.0021	0.0042
09/25/1999	EC-long	2298	4595	0.0098	0.0196
09/26/1999	EC-long	3939	7447	0.0159	0.0300
09/27/1999	EC-long	8711	6513	0.0359	0.0269
09/28/1999	EC-long	0	0	0.0000	0.0000
09/29/1999	EC-long	0	0	0.0000	0.0000
09/30/1999	EC-long	0	0	0.0000	0.0000
10/02/1999	EC-long	0	0	0.0000	0.0000
10/03/1999	EC-long	13683	11862	0.0550	0.0475
10/05/1999	EC-long	4625	9250	0.0186	0.0373
10/09/1999	EC-long	5313	8315	0.0215	0.0336
10/10/1999	EC-long	3425	6850	0.0139	0.0277
10/11/1999	EC-long	4375	8750	0.0176	0.0353
10/13/1999	EC-long	0	0	0.0000	0.0000
10/14/1999	EC-long	0	0	0.0000	0.0000
10/16/1999	EC-long	8818	6256	0.0361	0.0254
10/19/1999	EC-long	5103	7927	0.0205	0.0320
10/20/1999	EC-long	12811	19318	0.0516	0.0779
09/04/1999	EC-short	2692	2427	0.0101	0.0110
09/05/1999	EC-short	2506	2697	0.0106	0.0097
09/07/1999	EC-short	2598	2385	0.0106	0.0103
09/08/1999	EC-short	5290	2485	0.0217	0.0129
09/09/1999	EC-short	3029	3232	0.0122	0.0098
09/10/1999	EC-short	2800	2270	0.0116	0.0090
09/11/1999	EC-short	0	0	0.0000	0.0000
09/13/1999	EC-short	0	0	0.0000	0.0000
09/14/1999	EC-short	0	0	0.0000	0.0000

10/02/1999	MS-long	28560	62309	0.1111	0.2411
10/03/1999	MS-long	59680	87528	0.2403	0.3382
10/05/1999	MS-long	51926	79301	0.2125	0.3110
10/09/1999	MS-long	91580	90221	0.3848	0.3861
10/10/1999	MS-long	76720	91994	0.3260	0.3957
10/11/1999	MS-long	90350	104936	0.3818	0.4432
10/13/1999	MS-long	82138	102672	0.3458	0.4291
10/14/1999	MS-long	83362	120160	0.3476	0.4856
10/16/1999	MS-long	108820	126689	0.4638	0.5519
10/19/1999	MS-long	76756	106831	0.3227	0.4400
10/20/1999	MS-long	106188	102090	0.4480	0.4441
09/04/1999	MS-short	3016	2759	0.0125	0.0117
09/05/1999	MS-short	3712	3521	0.0150	0.0145
09/07/1999	MS-short	4912	5006	0.0196	0.0204
09/08/1999	MS-short	6900	2697	0.0276	0.0103
09/09/1999	MS-short	2780	4426	0.0116	0.0189
09/10/1999	MS-short	2772	2258	0.0111	0.0090
09/11/1999	MS-short	0	0	0.0000	0.0000
09/13/1999	MS-short	0	0	0.0000	0.0000
09/14/1999	MS-short	0	0	0.0000	0.0000
09/15/1999	MS-short	2499	2790	0.0099	0.0110
09/16/1999	MS-short	1160	1963	0.0046	0.0076
09/17/1999	MS-short	7074	6190	0.0292	0.0269
09/18/1999	MS-short	5758	4535	0.0234	0.0185
09/19/1999	MS-short	6882	5396	0.0276	0.0215
09/20/1999	MS-short	4326	4549	0.0169	0.0174
09/21/1999	MS-short	1640	3667	0.0070	0.0156
09/22/1999	MS-short	1132	2089	0.0048	0.0089
09/23/1999	MS-short	2262	4313	0.0096	0.0184
09/24/1999	MS-short	4025	5619	0.0167	0.0236
09/25/1999	MS-short	1312	1608	0.0054	0.0066
09/26/1999	MS-short	1968	4401	0.0084	0.0187
09/27/1999	MS-short	4928	9662	0.0209	0.0412
09/28/1999	MS-short	1968	3712	0.0083	0.0158
09/29/1999	MS-short	4720	10554	0.0201	0.0450
09/30/1999	MS-short	8160	18024	0.0313	0.0692
10/02/1999	MS-short	5920	12150	0.0252	0.0518
10/03/1999	MS-short	44818	54020	0.1844	0.2251
10/05/1999	MS-short	45720	92708	0.1938	0.3952
10/09/1999	MS-short	71000	158761	0.3024	0.6762
10/10/1999	MS-short	84380	166788	0.3564	0.7117
10/11/1999	MS-short	70000	156525	0.2981	0.6667
10/13/1999	MS-short	79162	176002	0.3370	0.7497
10/14/1999	MS-short	85600	191407	0.3646	0.8153
10/16/1999	MS-short	109840	222666	0.4657	0.9495
10/19/1999	MS-short	92960	199150	0.3951	0.8487
10/20/1999	MS-short	109214	231402	0.4637	0.9864

10/20/99	MS-short	MS10	8.927	19638450
10/20/99	EC-long	EC1	7.546	16600550
10/20/99	EC-long	EC3	6.589	14495047
10/20/99	EC-long	EC4	7.226	15897793
10/20/99	EC-long	EC5	8.445	18578782
10/20/99	EC-short	EC6	5.691	12519581
10/20/99	EC-short	EC7	6.699	14738521
10/20/99	EC-short	EC8	7.929	17444411
10/20/99	EC-short	EC9	8.567	18847157
10/20/99	EC-short	EC10	9.026	19857024

EC-long	EC2	leaflets	F	0	0.0000	0.0	0.0000	0	0
EC-long	EC3	leaflets	F	0.0009	0.0000	0.0	0.0000	0	0
EC-long	EC4	leaflets	F	0	0.0000	0.0	0.0000	0	0
EC-long	EC5	leaflets	F	0.0111	0.0000	0.0	0.0000	0	0
EC-short	EC6	leaflets	F	0.0019	0.0000	0.0	0.0000	0	0
EC-short	EC7	leaflets	F	0.003	0.0000	0.0	0.0000	0	0
EC-short	EC8	leaflets	F	0.008	0.0000	0.0	0.0000	0	0
EC-short	EC9	leaflets	F	0	0.0003		0.0003	0	702
EC-short	EC10	leaflets	F	0	0.0000	0.0	0.0000	0	0
MS-long	MS1	green-tips	F	0	0.0100		0.0100	0	21,943
MS-long	MS2	green-tips	F	0.0816	0.1867	2.3	0.1867	5,032,810	410,677
MS-long	MS3	green-tips	A+F				0.0221	0	48,713
MS-long	MS4	green-tips	A+F				0.2866	0	630,630
MS-long	MS5	green-tips	F	0.0237	0.0000	0.0	0.0000	0	0
MS-short	MS6	green-tips	F	0.0299	0.0066	0.2	0.0066	484,351	14,482
MS-short	MS7	green-tips	F	0.0568	0.0353	0.6	0.0353	1,366,003	77,589
MS-short	MS8	green-tips	F	0.0446	0.6637	14.9	0.6637	32,738,723	1,460,147
MS-short	MS9	green-tips	F	0.0002	0.0045	22.7	0.0045	50,029,082	10,006
MS-short	MS10	green-tips	F	0.0228	0.0000	0.0	0.0000	0	0
MS-long	MS3	green-tips	A	0.0497	0.0090	0.2	0.0090	399,117	19,836
MS-long	MS4	green-tips	A	0.0227	0.2277	10.0	0.2277	22,066,309	500,905
MS-long	MS3	green-tips	F	0.0178	0.0131	0.7	0.0131	1,622,272	28,876
MS-long	MS4	green-tips	F	0.0074	0.0590	8.0	0.0590	17,530,342	129,725
MS-long	MS1	wall		29	0.0000	0.0	0.0000	0	0
MS-long	MS2	wall		29.8	0.0000	0.0	0.0000	0	0
MS-long	MS3	wall		30	0.0000	0.0	0.0000	0	0
MS-long	MS4	wall		28.9	0.0000	0.0	0.0000	0	0
MS-long	MS5	wall		30	0.0003	0.0	0.1504	614	330,928
MS-short	MS6	wall		29.5	0.0000	0.0	0.0000	0	0
MS-short	MS7	wall		29	0.0000	0.0	0.0000	0	0
MS-short	MS8	wall		30.3	0.0000	0.0	0.1085	0	238,741
MS-short	MS9	wall		29.5	0.0000	0.0	0.0000	0	0
MS-short	MS10	wall		28.9	0.0003	0.0	0.1449	614	318,794
EC-long	EC1	wall		29.8	0.0001	0.0	0.0640	263	140,881
EC-long	EC2	wall		30	0.0000	0.0	0.0000	0	0
EC-long	EC3	wall		30	0.0000	0.0	0.0000	0	0
EC-long	EC4	wall		30.2	0.0000	0.0	0.0000	0	0
EC-long	EC5	wall		29.5	0.0002	0.0	0.1057	439	232,437
EC-short	EC6	wall		30	0.0001	0.0	0.0645	263	141,826
EC-short	EC7	wall		29.5	0.0000	0.0	0.0000	0	0
EC-short	EC8	wall		30.5	0.0000	0.0	0.0000	0	0
EC-short	EC9	wall		29.2	0.0000	0.0	0.0000	0	0
EC-short	EC10	wall		30	0.0000	0.0	0.0000	0	0
MS-long	MS1	spm			0.0000	0.0	0.0000	0	0
MS-long	MS2	spm			0.0005	0.0	0.0199	1,141	43,885
MS-long	MS3	spm			0.0000	0.0	0.0000	0	0
MS-long	MS4	spm			0.0000	0.0	0.0688	0	151,404
MS-long	MS5	spm			0.0000	0.0	0.0000	0	0
MS-short	MS6	spm			0.0000	0.0	0.0000	0	0
MS-short	MS7	spm			0.0000	0.0	0.0289	0	63,633
MS-short	MS8	spm			0.0012	0.0	0.0938	2,545	206,260
MS-short	MS9	spm			0.0000	0.0	0.0000	0	0
MS-short	MS10	spm			0.0000	0.0	0.0000	0	0
EC-long	EC1	spm			0.0000	0.0	0.0000	0	0
EC-long	EC2	spm			0.0000	0.0	0.0000	0	0
EC-long	EC3	spm			0.0000	0.0	0.0000	0	0
EC-long	EC4	spm			0.0000	0.0	0.0000	0	0
EC-long	EC5	spm			0.0000	0.0	0.0000	0	0
EC-short	EC6	spm			0.0000	0.0	0.0000	0	0

EC-short	EC6	9/15-root-water		0.0489		0.0489		107,597
EC-short	EC7	9/15-root-water		0.1503		0.1503		330,763
EC-short	EC8	9/15-root-water		0.2556		0.2556		562,359
EC-short	EC9	9/15-root-water		0.2217		0.2217		487,774
EC-short	EC10	9/15-root-water		0.5082		0.5082		1,117,961

11/17/99	EC 3	24.260	0.576	4.348	18	35.8	2.318	0.14
11/17/99	EC 11	20.462	0.669	5.461	27	33.9	2.257	0.15
12/05/99	EC 14	18.763	0.432	2.608	14	36.4	2.066	0.14
12/05/99	EC 7	24.555	0.501	3.443	14	36.9	2.19	0.14
12/05/99	EC 4	24.461	0.397	2.183	9	38.9	2.314	0.11